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CONTENTS

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BIOTIC COMMUNITIES OF KAIBAB PLATEAU, ARIZONA*

D. IRVIN RASMUSSEN

* The material here presented is included in a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Graduate School of the University of Illinois. Contribution from the Zoological Laboratory of the University of Illinois, No. 587.

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I. INTRODUCTION

The recognition of the spatial agreement of many plant and animal communities and their consideration as biotic communities has been a recent development in biological fields. Plant communities have been studied without attention to the animals, but the investigations of terrestrial animal communities without some consideration of plants is practically impossible. Therefore, the necessity for animal ecologists to recognize the importance of plants has given the study of bio-ecology its greatest impetus.

The animal communities of a deciduous forest from the early developmental stages to the climax have been described by Shelford ('13), and the plant and animal communities were shown to be in agreement. In "an associational study of Illinois sand prairie" Vestal ('13) concluded that animals and plants in any terrestrial environment are very intimately related, and the animal and plant communities are coextensive and may be considered together as a biotic "association" (community). The papers of Weese ('24), Blake ('26), Bird ('29), and others have all shown the close relationship of plant and animal communities.

In recent bio-ecological studies there has been a change in methods with greater interest in use of quantitative measurements to improve the quality of field observations. The papers cited are examples of such an approach.

This type of study has dealt in the main with the smaller species present on an area. None of the investigations were concerned with an original fauna in its entirety. The locations of study areas have precluded that.

This paper deals with the results of a study of land communities and their habitats. It is not only concerned with the smaller species, but an attempt is also made to apply quantitative methods of study to a number of large and influent native species. The area studied has been widely advertised because of its larger endemic animals. Also, man, in an attempt to increase the numbers of certain native species here, has greatly modified the biota of the area. The study was undertaken because of interest in the variations in numbers of the large native species.

The terms and concepts of Shelford ('26) have been used following their use by Smith ('28) and Bird ('29). The study concerns larger areas and grosser features, which accounts for not using a number of the terms. One modification of the term "influent" is used in designating those larger animals that have relations of major importance in the biotic balance and in the community, the *Major Influents*. The importance of the animal within the community is the criterion used. It is not limited by year-long residence or seasonal occurrence.

II. PHYSICAL ENVIRONMENT

Physiography

This study was conducted on the Kaibab Plateau in Coconino County in extreme northern Arizona. This is located in what is known as the Grand Canyon section of the Colorado Plateau Province. It is unique in being the largest and best-defined of the block plateaus and one of the very few that is bounded on all sides by escarpments and slopes which descend to lower lands. It is enclosed between meridians 111° 50′ and 112° 40′, and parallels 36° 5′ and 37°. (Figs. 1 and 2. The area is included in the Kaibab and Echo Cliffs sheets of the United States Geological Survey. It has a maximum length of sixty miles (95 kilometers) and a maximum width of thirty-five miles (55 km.). The plateau proper consists of approximately 1,152 square miles (2,980 square km.) which are above 6,000 feet (1,830 meters). The highest point has an elevation of 9,200 feet (2,800 m.). On the extreme west side there is an area of nearly 120 square miles (310 square km.) above the upper rim of Kanab Creek, but below the 6,000-foot (1,830 m.) contour. The plateau is bounded on the south by the Grand Canyon of the Colorado River along the region of its greatest magnitude and outstanding scenic grandeur. The elevation of the southern rim of the plateau varies from 8,800 feet (2,680 m.) to slightly less than 6,000 feet (1,830 m.), and is 6,550 (2,000 m.) to 3,800 feet (1,150 m.) above the Colorado River. The canyon rim itself is five to ten miles (8 to 16 km.) back from the river, the area between the rim and river being made of precipitous walls of hard strata several hundred feet thick, with slopes and platforms where the softer strata have receded toward the rim. The most extensive platform is the Esplanade, so named by Dutton ('82), and called "Sand Rocks" by the local cowboys. This has resulted from the weathering back of the Hermit shale, leaving a hard layer of Supai or Permian sandstone exposed. This conspicuous red sandstone, with the great breadth of exposure, is the outstanding feature of the canyon landscape in the western portion of the canyons that border the plateau. It has an elevation of approximately 4,000 feet (1,220 m.).

Kanab Creek Canyon, a miniature Grand Canyon of itself, marks the extreme western boundary of the plateau, its high perpendicular walls forming a natural barrier to movement of most animals. A north and south fault parallel to Kanab Creek, but sixteen miles (26 km.) to the east, marks the approximate west boundary of the higher portions of the plateau. This fault line, north of Snake Gulch (near Ryan), tends toward the east, marking the northwestern boundary of the plateau proper; the plateau ends where this joins the line of escarpment that runs north along

the eastern border. The eastern boundary is marked by a great monoclinical fold, the strata dipping down 2,000 to 3,000 feet (610 to 915 m.) to form the Marble platform. This region is called Houserock Valley.

The surface of the plateau is surprisingly level and although partially dissected, there are no large canyons near the summit. Around the edges are steep, rugged canyons, and in this region it is the canyons and not the peaks that are the outstanding feature of the topography.

A thick layer of porous Kaibab limestone of Permian age covers the plateau. The presence of this type of terrain accounts for the fact that although higher portions of the plateau receive nearly 30

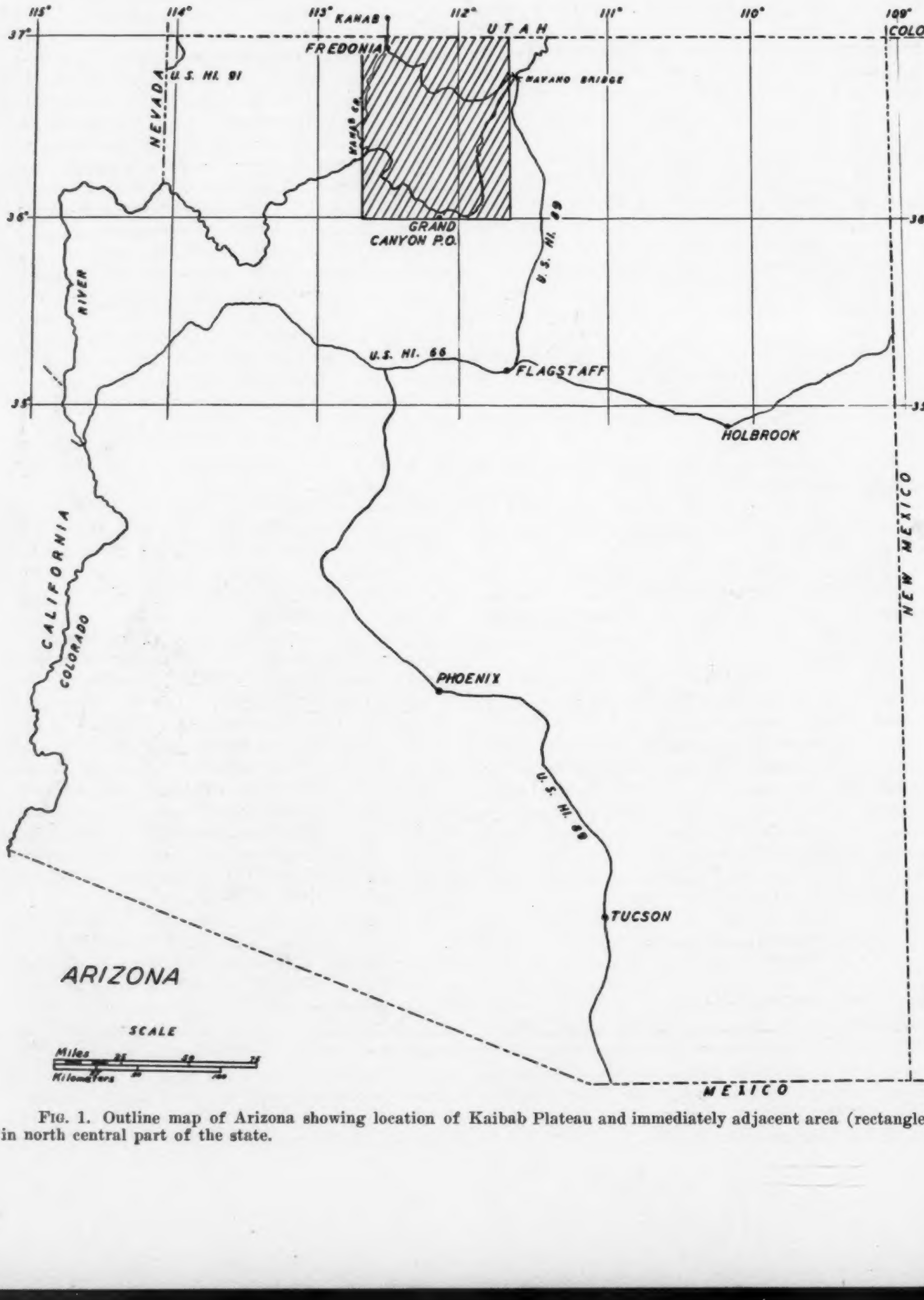

Fig. 1. Outline map of Arizona showing location of Kaibab Plateau and immediately adjacent area (rectangle) in north central part of the state.

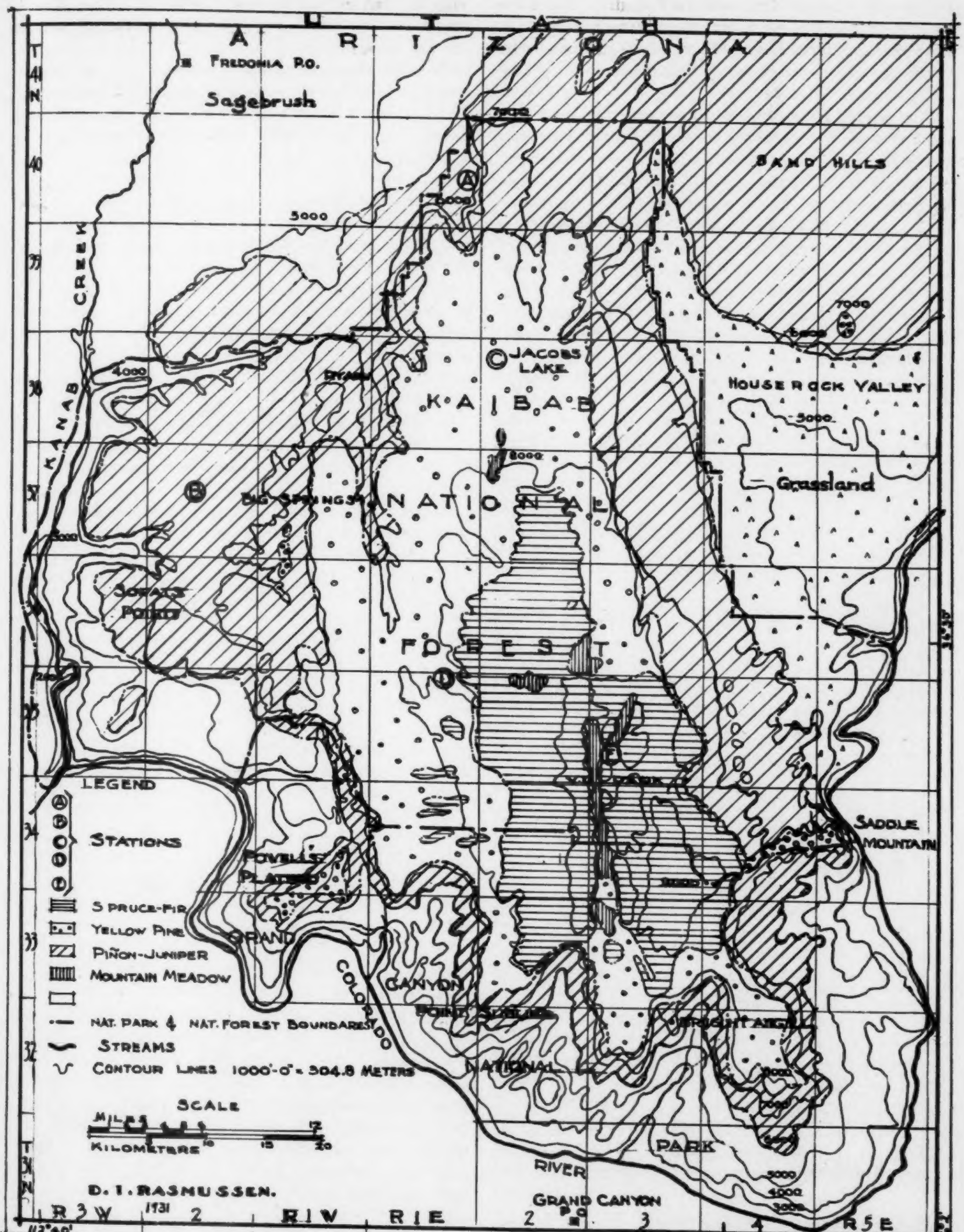

FIG. 2. Map of Kaibab Plateau, Arizona, showing townships, general vegetational types, locations of five study stations (A, B, C, D, E), 1,000-foot (304.8 m.) contours, and Kaibab National Forest and Grand Canyon National Park boundaries.

inches (75 cm.) of precipitation annually, there are no streams. Even after the melting of snow in the spring, or after the heavy rains of late summer, there is no run-off and very rarely erosion caused by running water.

The porous condition of the ground not only prevents run-off, but accounts for the scarcity of springs and bodies of water. A typical form of topography is evident in the presence of "sink holes," circular-shaped areas into which water drains during storms and where it sinks downward. Some few of these sink holes have become sealed by accumulation of fine soils, and the water is retained. Such small ponds of water, of ten to one hundred feet (3 to 30 m.) in diameter, are locally called "lakes." They are practically the sole source of water for all the animals. They are not abundant, and it is often several miles between them.

CLIMATE

The climate of the Kaibab Plateau is decidedly moist in relation to the surrounding region. The only yearly climatological records that exist for the plateau are for the Bright Angel Ranger Station, at an elevation of 8,400 feet (2,560 m.) and situated near the southern tip of the plateau. These records show an average annual precipitation of 26.57 inches (67.48 cm.) for the period 1925 to 1936, inclusive. Snows are heavy in winter, often with a depth of eight to ten feet (2.5 to 3 m.) occurring on the higher portions. The typical summer consists of a dry foresummer, followed by months of greatest rainfall (Fig. 3, III). June is the dry month of the year. May is usually dry, as is early July. Then storms are, as a rule, regular until early September; showers occur several times each week during the afternoon or evening and are often accompanied by violent electrical disturbances. The distribution of the summer showers is spotted, and the regions surrounding the plateau are usually untouched by moisture. On the highest portions of the plateau the precipitation from early October to late April occurs as snow, and snowstorms often occur in May and September. October and November are comparatively dry, and February is the month with the greatest amount of precipitation. Temperature records show only two months, July and August, with a mean temperature over 59° F. (15° C.) and show four months, December to March, inclusive, with a mean temperature below 32° F. (0° C.).

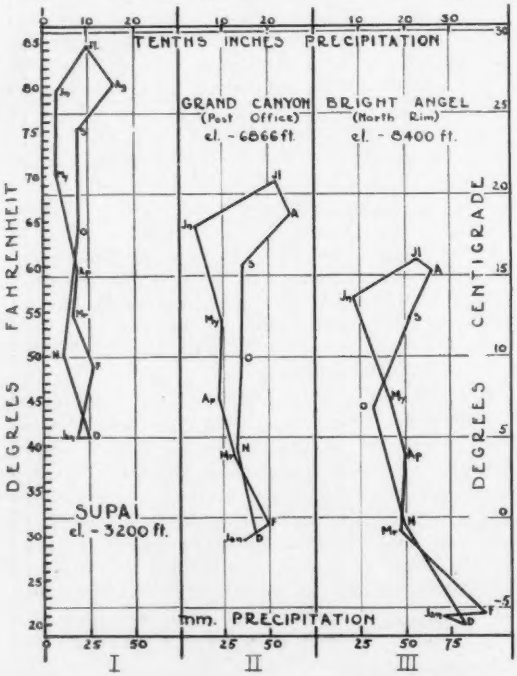

FIG. 3. Climographs of three weather stations located nearest the Kaibab study area. *I* is Supai, elevation 3,200 feet (975 m.), records 21 years to April, 1923, when it was discontinued. *II* is Grand Canyon, Arizona, elevation 6,866 feet (2,093 m.), records 28 years to 1937. *III* is Bright Angel, elevation 8,400 feet (2,560 m.), records 12 years (incomplete), 1925-37.

Table 1 shows monthly precipitation and temperature records at Bright Angel Ranger Station near the southern edge of the plateau and the two other nearest weather stations, i.e., Grand Canyon, Arizona, on the south rim of the canyon and Supai, twenty-four miles (38.60 km.) west and south of Grand Canyon postoffice and within the canyon. Figure 3 consists of three climographs based on available climatic data of these three stations. The graphs, in addition to showing the regular seasonal march of temperature and moisture, illustrate the marked differences in monthly precipitation and temperature associated with elevation differences.

TABLE 1. Climatic data Arizona stations.
El. Elevation in feet; P, Average monthly precipitation from available records; T, mean monthly temperature from available records.

	SUPAI El. 3,200 feet Records 21 years to April 1933 (Station discontinued)		GRAND CANYON El. 6,866 feet Records 29 years to January 1937		BRIGHT ANGEL El. 8,400 feet Records 12 years (incomplete) 1925-36, inclusive	
	P	T	P	T	P	T
January	.73	42.2	1.44	29.1	2.88	21.2
February	1.08	48.0	1.91	32.8	3.76	22.9
March	.63	54.5	1.28	38.0	1.96	31.5
April	.71	58.8	.88	45.3	1.94	38.4
May	.29	69.9	.95	53.4	1.62	46.2
June	.31	79.3	.39	63.1	.92	57.9
July	.94	83.0	2.16	68.7	2.26	61.7
August	1.55	80.8	2.44	66.5	2.63	59.3
September	.75	75.1	1.35	60.4	2.11	53.3
October	.75	63.0	1.38	49.5	1.34	43.6
November	.42	50.4	1.28	39.2	1.92	32.4
December	.99	42.0	1.61	30.6	3.23	20.1
Total precipitation	9.15	....	17.07	....	26.57	....
Monthly mean temperature	....	62.3	....	48.0	....	40.7

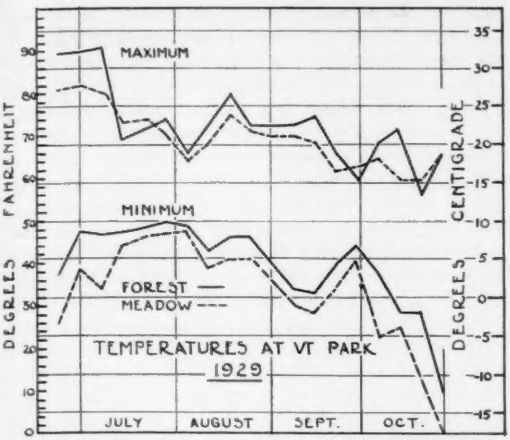

FIG. 4. Weekly maximum and minimum temperatures of spruce-fir forest and meadow, VT Park, 1929.

Figure 4 shows summer temperature records (weekly maximum and minimum) for the summit of the plateau. These previously unpublished data were secured during 1929 at VT Park, elevation 8,900 feet (2,715 m.), by Pauline Mead. They show the temperature range in the open park or meadow and the bordering spruce-fir forest.

III. HISTORY

AREA

The individuality and distinctive boundaries of the Kaibab Plateau, usually referred to as just the "Kaibab," have made it an entity in the records and stories of both white men and Indians, and reference to this area is not often confused with any other.

The plateau and the adjoining Grand Canyon have an important part in the legends and stories of the neighboring Indian tribes. The existence of an impassable barrier and the value of a productive hunting-ground in this arid region can well explain the importance with which it has been regarded by these people.

Thus, when the first whites, who were Mormon pioneers from the north, visited the territory in the late 1850's, they found the region famous in Indian tradition and of considerable economic value. The area was the summer home for the Kaibabits, a division of the Piute Indians of southern Utah. The plateau was the fall meeting place for the Piutes, the Navajoes, and often other southwestern tribes. Their primary purpose in assembling was to obtain deer hides or buckskin, which was a main article of commerce. They also came to the plateau to hunt on this neutral hunting-ground, to play games of chance, and to trade with the other tribes. A great deal of the early history of the plateau is reflected in the name "Buckskin Mountain," the name that the first white settlers gave it and by which it is still known locally.

The amount of early hunting on the plateau can only be judged from verbal reports of "old-timers" of the region, both Indians and whites. A number of old residents are very well informed in Indian history and an attempt was made to check various sources of information of this nature.

I am indebted for much of the information concerning early Indian hunting to Mr. Billy Crosby, a local cowboy who speaks the Indian language fluently and is well acquainted with the older Indians. Information was also obtained from Mr. D. A. Riggs, one of the men who assisted Major Powell in the Government Survey of the region in the early 1870's.

The Indians were primarily interested in deer for hides, and although a few were killed in all seasons, the bulk were killed in the fall, when the hides were thickest and best. The Piutes and the Navajoes, especially the latter, have always been great rabbit eaters, and the blacktailed jack rabbit, *Lepus californicus*, was their main source of meat, venison being only of minor importance. The Kaibabits did most of the deer hunting. The total of individuals in the clan averaged only about five hundred Indians, and not more than two hundred of these were men who would take part in hunting. The Navajoes were not especially interested in hunting but bargained for the buckskin of a goodly portion of what the Piutes killed. Crosby estimates that the Piute Indians did not average more than three deer each during the fall hunt, and that in the neighborhood of 100 were killed by them during the summer. He also estimates that the Navajoes did not kill more than a hundred deer in the fall. This would make a total for the maximum kill of 800 deer killed per year by Indian hunting, and perhaps a figure less than that for the average kill. The hides were saved to be tanned; the meat was "jerked," i.e., cut in strips, dried on the ground, and then transported to the lower country to be used as provisions.

The mountain lion was not molested by the Indians, and only occasionally did they kill bobcats or coyotes. The Navajoes never killed coyotes because of a religious taboo.

In 1870, the year following his first descent of the Colorado River, Major John Wesley Powell began the first government exploration of the country north of the Grand Canyon. In the report written in 1875 he says, "The most elevated portion of the country is a central belt, about twenty-five or thirty miles in width and about eighty miles in length. This is called by the Indians Kaibab, or 'mountain lying down,' and we have adopted the name." (Powell, '75, p. 185.) In 1880 and 1881 the region was thoroughly explored and described in detail by Dutton ('82).

"The earliest indicated extensive use of the Kaibab Plateau for livestock was in 1885 and 1886, when 2,000 cattle were placed there." (Mann and Locke, '31). Dutton ('82) comments about wild cattle present on the plateau. These were apparently a small number of feral and semi-wild animals, originally

from herds in surrounding lowlands. "In 1887 and 1889 at least 200,000 sheep and 20,000 cattle and many horses were using the range and surrounding desert," state Mann and Locke ('31); information gained from stockmen indicates that at that time the Kaibab was considered as having an unlimited supply of forage for livestock. The result was that the plateau had its first known overpopulation in excessive herds of cattle, horses, and sheep.

Dutton ('82, p. 137) describes the forest at the time he saw it: "There is a constant succession of parks and glades—dreamy avenues of grass and flowers winding between sylvan walls or spreading out into broad open meadows. From June until September there is a display of wild flowers quite beyond description." These conditions have never been repeated, except in part, since the livestock entered and remained there. The number of livestock that have used the area in recent years, according to available United States Forest Service records, is shown in Figure 5.

On February 20, 1893, by proclamation of President Benjamin Harrison, the Grand Canyon Forest Reserve was created, including the Kaibab Plateau, the Grand Canyon, and the adjoining area on the south rim. On November 28, 1906, President Theodore Roosevelt created the Grand Canyon National Game Preserve, which included approximately the same territory as is now in the Kaibab National Forest and the Grand Canyon National Park north of the Colorado River. He also created the Grand Canyon National Monument by proclamation of January 11, 1908, and by the same means established the name of Kaibab National Forest for the area north of the Grand Canyon, July 21, 1908. By Act of Congress, February 26, 1919, the Grand Canyon National Park was created and made to include approximately the southern fourth of the plateau. In 1927 an additional 46,000 acres (18,600 hectares) was added to the national park from the national forest area. The present area of the national park north of the Colorado River is approximately 346,000 acres (140,100 ha.) and of the Kaibab National Forest, north of the Colorado River, 706,000 acres (285,800 ha.).

DEER HERD

The history of the deer herd since the establishing of the game preserve in 1906, up until the early 1930's, has been a story of conflicting interests, associated with a general misunderstanding of true field conditions.

The story of the population change as interpreted at the present time is: with the creation of the game preserve, the killing of deer was prohibited. At the same time there was a marked decrease in numbers of domestic sheep, grazed on the area. From 1906 to 1923 government hunters were employed in killing predatory mammals. During the period 1906 to 1931, 781 mountain lions, 30 wolves, 4,889 coyotes, and 554 bobcats were trapped or shot (Fig. 5, II). Total removal 1906 to 1939 inclusive has been 816 mountain lions, 30 wolves, 7,388 coyotes and 863 bobcats. The removal from 1931 to 1939 inclusive has been by hunting lions for sport and coyotes and bobcats for fur. This resulted in extermination of wolves and definite reduction in other species. The decrease in competition for forage, the check on natural enemies and the prevention of killing by man caused an increase in the deer herd in this ideal deer range. The deers' habits and the topography of the country prevented a scattering of deer to adjacent ranges. The increase was allowed to go on without check for sixteen years, until the estimated 4,000 of 1906 had

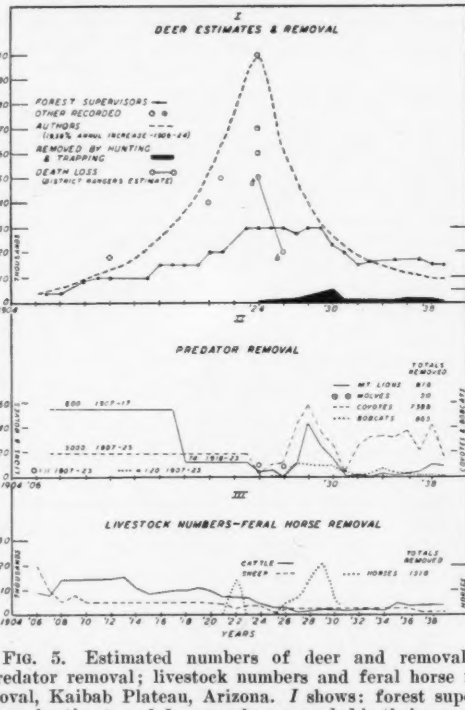

FIG. 5. Estimated numbers of deer and removals; predator removal; livestock numbers and feral horse removal, Kaibab Plateau, Arizona. *I* shows: forest supervisors' estimates of deer numbers recorded in their annual reports based on general estimates previous to 1930, since 1930 based on organized winter counts: also estimated numbers obtained from reports of men visiting the Kaibab Plateau to make observations on the deer. The death loss of 1924-26, record (line a—b) is based on a report by United States Forest Service Ranger Benjamin Swapp, who was in charge of the area where the deer died. The broken line represents an estimated population trend from 4,000 deer in 1906 to near 100,000 in 1924. This represents an accumulative annual increase of 19.58%. Following 1924 a decrease took place due to the die-off, until there was an estimated 20,000 in 1931, and less than 10,000 in 1939. The shaded portion indicates the total removal from hunting, trapping, and fawn removal during the period. *II* gives record of predator removal in the period 1906-39. No lions and very few coyotes were removed in 1931, although trapping for fur and hunting of mountain lions for sport has continued since that date. *III* shows number of livestock permitted on the area from all available Forest Service records and the number of feral or wild horses removed by hunting during the period of 1922-39 inclusive.

become an enormous herd of near 100,000 in 1924. The peak was reached, the range depleted, and the deer population started downhill. There were deaths by thousands from malnutrition and related causes. In 1924 hunting was permitted on the national forest, and an average of near 1,000 deer was removed each year for five years, then 4,400 in 1929, and 5,033 in 1930. During this time the herd decreased to an estimated 20,000. The range had been so severely damaged that 20,000 was an excessive population from the standpoint of condition of forage species. The herd has continued to decrease slowly until an estimated 10,000 were present in 1939.

Figure 5 shows the numbers of large mammals and removals from the Kaibab Plateau for the period 1906 to 1939. I shows the forest supervisor's estimates of deer numbers, recorded estimates of deer numbers from other observers, author's estimate, and hunting removal. The curve extending from 4,000 in 1906 to 100,000 in 1924 equals an annual accumulative increase of 19.58 percent. In the period previous to 1931 a total of 17,844 deer were removed as follows: 13,576 by sportsmen hunting, 1,124 hunting by government employees, 674 by trapping, and 2,470 caught as newly born fawns; 9,372 deer have been removed by sportsmen hunting in the period 1931 to 1939 inclusive.[1] II shows the number of mountain lions, wolves, coyotes, and bobcats removed from the area. III shows the number of sheep and cattle permitted on the area and the number of wild or feral horses killed.

The combination of a national game preserve and a national forest covering the same area and set apart before the creation of the state in which it is located, created a unique situation in administration. The United States Forest Service was in control of the major part of the area and initiated a game management program for their area, although one point in dispute with the State of Arizona (regarding the right to kill deer on that area) was taken to the United States Supreme Court. That Court ruled the Forest Service had the right to remove deer and under this ruling they conducted the so-called "government killing" in December, 1928. Six hundred and seventy-six does and 448 bucks were killed at this time by Forest Service officials following the regular hunt.

The southern end of the plateau is included in the Grand Canyon National Park and neither trapping nor hunting of deer has been allowed on this area. Objections were raised to hunting near the park because the park boundary was not a barrier to deer movement.

Range damage by deer was first recognized by Forest Service officials in 1918 in the Forest Supervisor's report. The first of many investigations was made in April, 1920, by S. B. Locke, then of the United States Forest Service. A memorandum of this visit is the first definite record of the maladjustments within the area. The problem of overpopulation of deer, however, was entirely new at that time. Knowledge of the habits and life history of deer and their relationship to other animals and to the forage was very meager.

A criticism of lack of knowledge of the Kaibab deer herd was made by Hough ('22), a journalist, in his impression of the Kaibab, and at that time this appeared as a justifiable criticism of both the state and several federal agencies concerned with the area. This was reflected in the very definite difference of opinion between personnel of the agencies as to what the true situation was and what should be done about it.

The necessity of limiting deer numbers was first realized by the Forest Service officials. When the information was made public, a storm of protest arose, mostly based on preconceived prejudices and misunderstandings. The very unusual appearance of many hundreds of these animals in the high meadows during the summer was a sight that could not be duplicated. Interference in any way with this scenic attraction was strongly objected to. Unfortunately, the facts in the matter were not understood nor accepted by all individuals and certain individuals spoke with authority about the area on the basis of a hurried trip along the summit of the plateau in summer. Many thought the reports of conditions to be exaggerated because they were given by a group whose major interest was believed to be the vegetation, and those interested solely in the display value failed to see the complex and far-reaching effect of maintaining such a large herd of deer.

An example of an observer not directly concerned with the controversy, but appreciating the seriousness of the conditions, was contained in a report on the area by George Shiras, III ('24), a naturalist who had wide experience in the study of deer, elk, and moose, and who, concerning a visit to the Kaibab in September, 1923, says, "Never before have I seen such deplorable conditions," and "but one conclusion could be reached, that from 30,000 to 40,000 deer were on the verge of starvation both in their summer and winter range." This statement was verified by the estimated loss of sixty percent of the total herd in the winters of 1924-25 and 1925-26 as estimated by Ranger Benjamin Swapp (Fig. 5, I, line a—b), the individual best acquainted with winter conditions at that time. (Forest Supervisor's Report of 1926.) And at this same time there were very serious objections raised by well-meaning individuals to removal of any of the animals from this area.

Two committees of non-Forest Service men, appointed by the United States Secretary of Agriculture, made investigations in 1924 and again in 1931. They were present for ten days each time, covered the plateau thoroughly and left complete records of conditions. In each case, the seriousness of the situa-

[1] The hunting removal by sportsmen since 1930 has been: 1931, 965; 1932, 640; 1933, 859; 1934, 1,035; 1935, 874; 1936, 1,433; 1937, 1,456; 1938, 1,395; 1939, 715; from United States Forest Service Records.

tion and the depleted conditions of the range were definitely recognized.

It is not believed that the controlled hunting on the National Forest has been the major cause of the great reduction in deer numbers. The greatest decrease took place before this could have been effective. Also, examination of winter ranges definitely indicates that the reduction occurred on the national park portion of the plateau, where no hunting was allowed, as well as on the national forest (Fig. 5).

The Kaibab deer herd has, however, focused attention to the problem of maladjustments in numbers of large native mammals. It can be credited with creating much interest in these problems and influencing the recent establishment in both the National Park Service and Forest Service of administrative divisions to study and act on such problems.

The problem of handling the Kaibab deer herd is not entirely solved at the present time. The existence of the one herd of deer on an area administered by two federal agencies which have distinct objectives and procedures will no doubt always result in certain differences. One of these agencies has as its major objective the preservation of natural conditions on the area under its control and this calls for a program of exclusion of domestic livestock, and protection of all the native animals. Thus no hunting or trapping of either deer, their predators or other animals of the area is permitted. The other agency has as its primary objective the management of the deer herd on the area under its control. This management program is to correlate deer numbers with the forage yield of the range, maintaining of a deer herd for its scenic value, to conduct a program of utilization by sportsman hunting and to correlate some use of the range by livestock with use by deer.

The dividing of the top of the Kaibab Plateau into two independent units from which there is no movement back and forth by the larger animals, either seasonally or year-long, appears to be impossible. On the basis of the present study the boundary established in 1928 between the Grand Canyon National Park and the Kaibab National Forest, although faulty in certain respects, approaches the aim of dividing the area into two fairly independent biological areas.

Extirpated and Introduced Mammals

The existence of areas that contain samples of all original fauna and flora are extremely rare, and the Kaibab is no exception in lacking some of the original larger species of animals. A list of names of mammals, birds, reptiles, and amphibians is given in the appendix of this paper.

Formerly the timber wolf occurred in limited numbers. The area appears to be well suited for this animal, but the existence of a small band of less than a dozen individuals was its status for many years. One of the local residents, well acquainted with early conditions, reports that during the early years of use of the Kaibab by livestock wolves killed a few cattle but they ate many more deer than cattle.

There are only four reported records of bear on the entire plateau in a period of at least eighty-five years, yet bear have always been present and are still found in southern Utah. Of these, three were *Euarctos americanus,* two black and one brown. All were killed on the summit of the plateau. According to reports believed to be authentic, a grizzly bear was killed by an Indian boy in South Canyon on the east side of the plateau about eighty-five years ago. This is the only record of this species reported by either Indians or whites.

The pronghorn antelope was formerly common in the grassland adjoining the plateau, but was exterminated soon after occupation of the area by white men.

Feral or wild horses have always been present on the Kaibab since the area was first used by domestic stock. The early cowboys claim they were not present before that time. Their number has been regularly added to by tame horses turning wild, and a few have been captured each year by cowboys. During the period from 1922 to 1931, 1,310 of these animals were killed on the National Forest in an effort to increase amount of food available for domestic livestock and deer (Fig. 5). In 1931 it was estimated that there were 200 remaining. These are among the most elusive of the wild animals of the plateau.

Feral burros were responsible for damage to native plants within the Grand Canyon, and elimination of several hundred individuals was deemed necessary by the National Park Service during the early 1930's.

Bison have been introduced into Houserock Valley on the east side of the plateau within recent years. The area there appears to be well suited to them, and they are making a rapid increase. There are no reports or records, however, of their former occurrence in this area.

IV. METHODS, SCOPE OF WORK, AND ACKNOWLEDGMENTS

Methods

The field work on which this study is based was carried on during June, July, and August of 1929, 1930, and in all months of 1931, except January and December. Intensive studies were carried out at five stations in typical plant communities:

(A)—Piñon-juniper area, north end of plateau, unbrowsed by deer.
(B)—Piñon-juniper area, west side of plateau, very heavily browsed by deer.
(C)—Yellow pine area, near Jacob's Lake, slightly browsed by deer.
(D)—Yellow pine area, near Dry Park, very heavily browsed by deer.
(E)—Spruce-fir area, near VT Park, very heavily browsed by deer.

Major quadrats of 2.50 acres (1 hectare) in area were established at these stations and were used as

bases for comparisons of the plants and animals of various areas. Random quantitative and qualitative samplings were made, supplemented by observations and cruising. The entire plateau was covered in a general reconnaissance in order to understand and correlate the findings of the smaller areas.

Collections of the invertebrate population were made from the ground surface, herbs, shrubs, and trees. In the collections from ground surface a metal cylinder, closed at one end, was used. This was 14.13 inches (36 cm.) in diameter and thus equaled 1/40,000 of an acre, or 1/100,000 of a hectare (King, '27; Bird, '29). In the other strata a sweep net was used. The methods were essentially the same as those of Weese ('24), Smith ('28), Shackleford ('29), and Bird ('29). The unit used here was fifty sweeps of an insect net of 30 cm. in diameter. Thus, a maximum unit collection consisted of fifty sweeps in trees, fifty sweeps in shrubs, fifty sweeps in herbs, and 0.1 m^2 of ground surface, including the needles and leaves. In the piñon-juniper the trees and shrubs were swept together. In the tabulation of data fifty sweeps were taken as representing the amount of life per square meter in the herb, shrub, and tree strata. Collections were made fortnightly, as nearly as possible. The circuit of the stations, however, exceeded one hundred and fifty miles, which was a limiting factor in this respect.

In the study of vertebrate numbers, considerable difficulty was experienced in arriving at numbers per unit area. A number of the methods reviewed and suggested by Taylor ('30) were used.

Practically each species of mammal called for a different technique in the estimation of population. The smaller nocturnal rodents and some nocturnal carnivores were obtained only by trapping. Golden mantled and antelope ground squirrels and chipmunks were trapped and counted by area counts. Use was made of staked areas and observations in early morning at time of their greatest activity. Presence of woodrats was indicated by the very obvious "rat sign" and trapping was used to check on numbers. The Kaibab woodrats' nests were easily seen and proved a reliable index of the rat population. Jack and cottontail rabbits were counted over large areas, and a number of pellet counts were made in definite small areas to determine relative abundance. Chickaree and Kaibab squirrel numbers were obtained by area counts. Signs of mammals were utilized in determining both relative numbers and distribution.

Many counts were made of Kaibab squirrels observed per mile along the highways and the numerous motor trails in the open stands of yellow pine. These counts showed remarkably uniform results when time of day and weather conditions were comparable. Maximum counts were obtained in very early morning, although evening counts gave very similar results.

Mule deer were seen in numbers of a few to several hundreds of individuals each day. Summer counts were conducted at various locations in the forests and open meadows or parks of the summer range. Regular morning and evening sex counts of deer visiting the open parks were made. The 1930 and 1931 total of these counts for the VT Park was 13,972 deer tabulated. These counts and the presence of tracks gave definite information on numbers and relative abundance in the various areas at different seasons. The presence of shed antlers gave information concerning distribution of bucks at the season the antlers are shed (usually February) on areas difficult to visit at that time.

Coyotes were often seen, heard, and tracked. Bobcats were tracked and a few individuals observed. Cougars, under natural conditions, were in evidence by "sign" only.

An estimate of the numbers of the more important birds was gained by counting singing males over definite areas. The relative abundance of birds apparently was best shown by use of the unit of time method of Grinnell and Storer ('24), with the modification of a unit of space as suggested by Dice ('30).

Tabulation of animal life of an area to obtain a reliable estimate of numbers involved is fraught with many difficulties. The variations in animal activities, different degrees of shyness, and many other factors are present. Estimates and counts by present methods may be filled with error, yet in population studies the statement, "the more strictly quantitative the work is, the better it is likely to be" (Shelford, '30), should be heeded.

In all censuses the large number of animals that were limited in their distribution by local habitat conditions was kept in mind, and in any area summaries corrections were made for this factor.

Calculations of areas were based on planimeter readings made from a United States Geological Survey map upon which was charted the major plant communities. Total animal numbers were calculated by a similar method.

ACKNOWLEDGMENTS

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I wish to acknowledge the assistance given by the following specialists without whose help and cooperation it would have been impossible to identify the material collected: Dr. R. V. Chamberlin, University of Utah (Chilopoda, Diplopoda, spiders); Dr. A. E. Emerson, University of Chicago (termites); Dr. M. R. Smith, A. and M. College, Mississippi (ants); Dr. Lee H. Townsend, University of Kentucky (ants); Dr. H. H. Ross, University of Illinois (saw-

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V. GENERAL COMMUNITY RELATIONSHIPS

The Kaibab Plateau, although surrounded by mile-deep canyons, desert grassland, or sagebrush plains, is almost entirely covered with trees. It has an extensive pygmy forest (piñon-juniper woodland) of *Pinus edulis*[2] and *Juniperus utahensis* extending around its edges and occurring at the lower elevations on the plateau summit. Above this is an area of nearly a pure stand of Rocky Mountain yellow pine, *Pinus brachyptera* (yellow pine consociation) extending as a belt around the summit of the plateau. This belt, although narrow at the southeastern border, is from 8 to 15 miles (13 to 25 km.) in width at the north and west sides. A large amount of Rocky Mountain quaking aspen, *Populus aurea,* is present in the upper half of this community.

The highest portions of the plateau are covered with a mixed coniferous forest of spruces, *Picea pungens* and *Picea engelmanni,* and firs, *Abies concolor, Abies lasiocarpa,* and *Pseudotsuga taxifolia,* with an interspersion of aspen. This montane forest, although definitely delineated and fairly uniform where it occurs, can hardly be referred to in its entirety as either the Petran montane forest, *Pinus-Pseudotsuga* association, or the Petran subalpine forest, *Picea-Abies* association, of Weaver and Clements ('29). It contains the characteristic species of both these climaxes.

A series of open parks or meadows occur on the summit of the plateau. These level areas are surrounded by montane forest, but contain only herbs and grasses.

Figure 6 shows the distribution and relative abundance of the dominant tree species on the plateau in relation to their occurrence at different altitudes. This is based on the number of trees with a d.b.h. (diameter breast height) of two inches (5.0 cm.) or over. Shrubs are not included in this comparison as they dominate only in very local situations.

There are, however, a series of discontinuous areas where scrub oak, *Quercus utahensis,* is dominant. These are situated, usually, at the border between the piñon-juniper and yellow pine communities and an average elevation of 6,800 to 7,000 feet (2,075 to 2,130 m.), on the steeper canyon walls and the plateau border. This Petran chaparral association fragment supports a relatively high population and variety of vertebrates and is considered in the vertebrate distribution study. The presence of the scrub

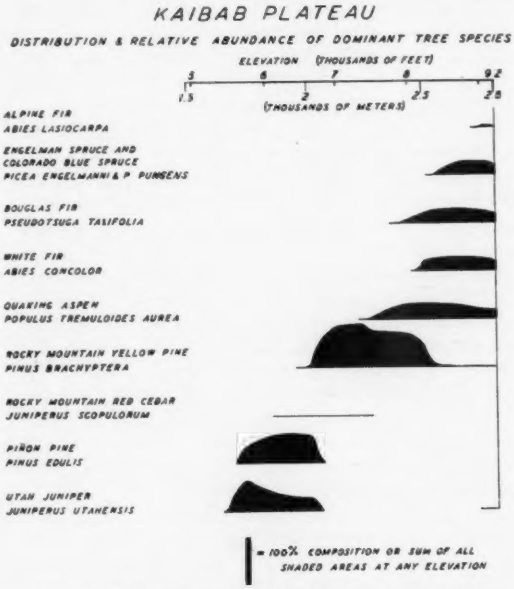

FIG. 6. Distribution and relative abundance of dominant tree species, Kaibab Plateau, Arizona. Total width of all shaded areas at any designated elevation equals 100% or total number of trees present.

oak alone, however, does not explain the distribution of these animals, and there are definite indications that the presence of cliffs, ledges, and steep canyon walls, occurring in much of the area where the oak and associated shrub species are found, is more important in providing favorable habitat conditions than the specific vegetation. Its presence on areas showing a steeper gradient than any other plant community on the Kaibab gives it undue emphasis when considered only from the altitudinal differences.

Table 2 shows a comparison of previous classifications of the vegetation of northern Arizona and plant distribution on the Kaibab Plateau. In the present discussion the forest above the piñon-juniper woodland is collectively referred to as the montane forest, and the distinctions between the yellow pine and mixed coniferous or spruce-fir forests are not considered marked enough to indicate different formations. This is based primarily on the fact that the distribution of the vertebrates on the Kaibab Plateau does not indicate two biotic communities of major importance. The vegetation has certain common characteristics (all is coniferous forest of very similar sized trees); has comparable subclimax stages (presence of aspen and forest parks in both communities);

[2] See appendix for the complete names of plants.

and the majority of vertebrate species and individuals present are not typical of either community.

Figures 7 and 8 show the distribution of mammals and amphibians and reptiles on the plateau. Table 3 gives the distribution and breeding records of birds.

TABLE 2. Plant communities compared with previous classifications of the vegetation of Northern Arizona. (Elevation in feet)

Kaibab Plateau	Clements (1920)	Shreve (1917)	Pearson (1920)	Merriam (1890)
	Alpine meadow climax	Alpine summits	Alpine zone above 11,500	Alpine zone above 11,500
				Sub-alpine or timber-line zone 10,500–11,500
Summit of Plateau 9200 Mixed coniferous (Spruce-fir) 8200–9200	Sub-alpine forest climax	Northern mesophytic evergreen forest	Engelmann spruce 9500–11,500	Hudsonian or spruce zone 9200–10,000
MONTANE			Douglas fir 8300–9500	Canadian or balsam fir zone 8200–9200
FOREST Yellow pine 6800–8200	Montane forest climax		Yellow pine 6700–8300	Neutral or pine zone 7000–8200 (Transition)
Woodland climax 5500–6800	Woodland climax	Western xerophytic evergreen	Piñon-juniper 5000–6700	Piñon zone 6000–7000 (Upper Sonoran)
Grassland climax 4000–5500 Sagebrush climax 4500–5500	Grassland climax	Desert grassland climax	Desert grassland 3000–5000	Desert area 4000–6000 (Sonoran)
	Sagebrush climax	Great Basin microphyll desert		

The mule deer (Fig. 7) summers and rears its young in the chaparral, yellow pine, and spruce-fir communities and winters in the piñon-juniper woodland. The selection is not indiscriminate, however, as the yellow pine is preferred by the does at the time fawns are born. Even with the presence of grassland, sage, and desert scrub communities within a short distance of the winter range, there is no marked movement of deer to these areas. The ranges of the coyote, the porcupine, and the most abundant animal of all, the tawny white-footed mouse, are not limited to any plant community or subclimax stage. This is also true of the two most abundant birds, the western chipping sparrow, the red-shafted flicker, and the most abundant reptile, the horned toad. In each case abundance is not uniform and some one or more communities are the regions of greatest abundance, either seasonally or year-long.

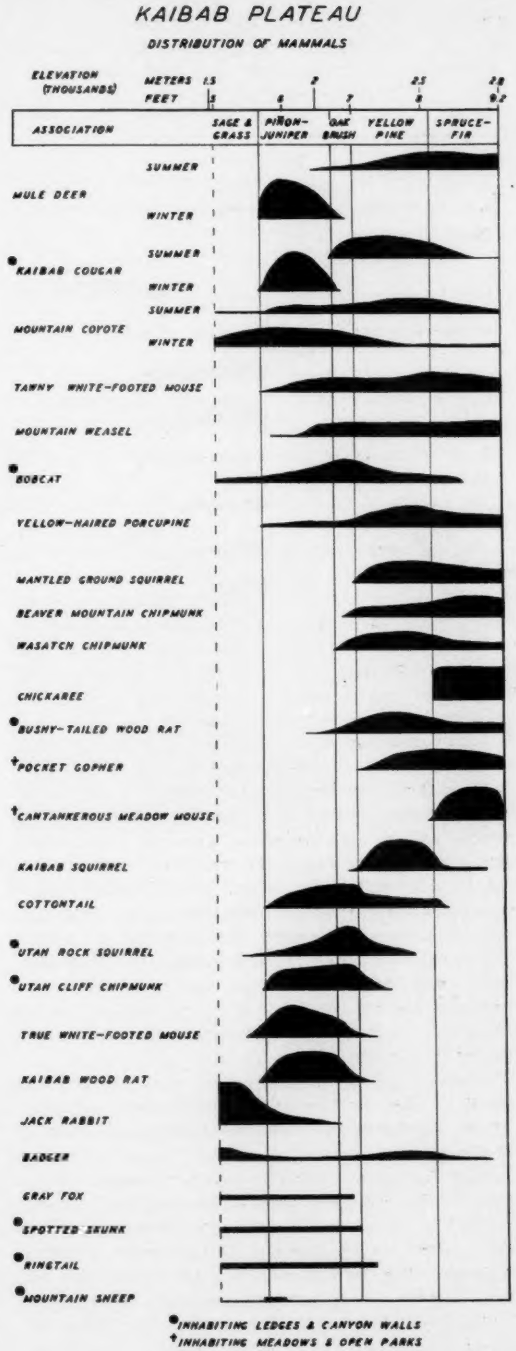

FIG. 7. Distribution of important and abundant mammal species, Kaibab Plateau, Arizona. Shaded areas for each species are of equal size (except four minor species) and represent total population and relative distribution on the plateau.

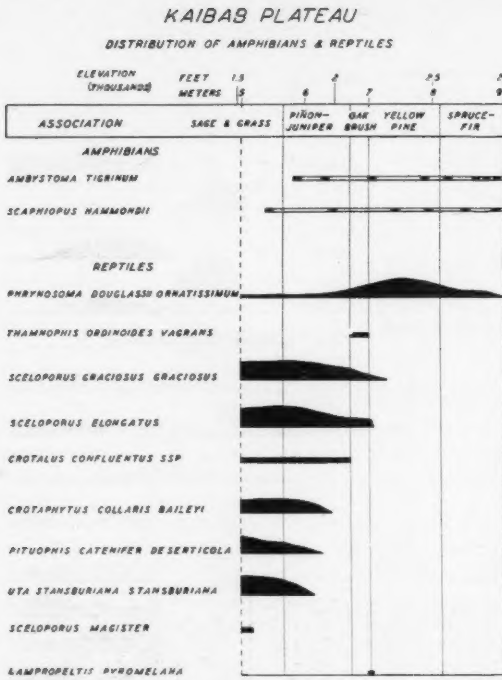

FIG. 8. Distribution of amphibians and reptiles on Kaibab Plateau, Arizona.

In the distribution of many smaller animals, numerous breeding birds and a large number of invertebrates, the plant communities are definitely recognized by the animals. They and the plants make up typical biotic communities of climax and seral rank. These are often greatly influenced by other vertebrates which ordinarily range over more than a single community. Such exceptions and irregularities do not invalidate the concept of a biotic community, but the criteria used in defining plant communities where dominants are sessile and the boundaries usually quite distinct, do not entirely suffice in the case of animals.

A continued, detailed study of plant communities, as such, leads to further divisions and consideration of smaller areas as distinct vegetational units. A study of the distribution of the larger and more influent animals, especially those of major importance (Major Influents) that exist at present only in limited areas and in unsettled regions, leads to the recognition of larger and more extensive units. A study of animal distribution of the Kaibab Plateau raises serious question regarding the rank of certain recognized plant formations as being true biotic formations, i.e., "biomes."

Four major biotic communities are recognized on the plateau, namely:

1. The *Pinus-Juniperus-Neotoma* association of the woodland climax

TABLE 3. Kaibab Plateau birds. Distribution of permanent and summer residents in relation to major plant communities. *, permanent residents; parallel line, abundant or common during breeding season; x, sparse and spotted distribution; N, nesting record; Y, juvenile (too young to have traveled far from nest). Average elevation of lower border of piñon-juniper is 5,500 feet, plateau summit is 9,200 feet.

Elevation	Ave. 5,500 feet (1,675 m.) ↓			Max. 9,200 feet (2,800 m.) →	
Plant Community	Sage-brush	Piñon-juniper	Oak-brush	Yellow pine	Spruce-fir
Turkey Vulture	x	x	x	x	x
*Western Goshawk				x N x	x x x
*Sharp-shinned Hawk					
*Cooper's Hawk	x	x	x	x	x
*Western Red-tailed Hawk	x		N		N N
Swainson's Hawk	x	x x			
*Prairie Falcon	x	x	x	x	x
*Ferruginous Rough-leg	x	x		x	
*Golden Eagle	x	x	x	x	
Desert Sparrow Hawk					
*Dusky Grouse				x	Y Y
*Gambel's Quail	x	N x			
Band-tailed Pigeon			x x x		
Western Mourning Dove		N	N		
*Horned Owl		x x	x	x	x
Nuttall's Poor-will		x			
Night Hawk		N			
White-throated Swift	x	x	x	x	x
Rufous Hummingbird			x	x	x
Broad-tailed Hummingbird			x	x N x	x x
Black-shinned Hummingbird		x x x	x x		
*Red-shafted Flicker		N		N N	N N N
*Lewis Woodpecker			x	x N	x
Natalie's Sapsucker				NNNN	NNNN
*White-breasted Woodpecker					N N N
*Batchelder's Woodpecker			x	x	x
*Alpine Three-toed Woodpecker					x N x N
Ash-throated Flycatcher		x	x		
Wright's Flycatcher				x	N x
Western Wood Pewee					
Olive-sided Flycatcher				x x	N
Violet-green Swallow				N N	N N N
Northern Cliff Swallow		x N x	x NN x		
*Long-crested Jay					Y
*Woodhouse's Jay		Y			
*American Raven	x	x			x x x
*Piñon Jay					
*Clark's Nutcracker				x	x x
*Mountain Chickadee			x	N	N N
*Gray Titmouse		N N			
*Lead-colored Bush-Tit		x x			
*Rocky Mountain Nuthatch				N N	x x
*Red-breasted Nuthatch					x x
*Pygmy Nuthatch				N N N	

TABLE 3. *(Continued)*

Elevation	Ave. 5,500 feet (1,675 m.) ↓			Max. 9,200 feet (2,800 m.) →	
Plant Community	Sage-brush	Piñon-juniper	Oak-brush	Yellow pine	Spruce-fir
*Rocky Mountain Creeper				x x x	x
Western House Wren			N x	N x	
*Cañon Wren	x	x x x	x x	x x x	
*Rock Wren	x	x N x	x	x	
Sage Thrasher	x				
*Western Robin		x x x	x x	N	N N N
Audubon's Hermit Thrush					N
Chestnut-backed Bluebird			x	N N	x
*Mountain Bluebird		x N x	N N	x x x	NNNN
Townsend's Solitaire				x	x x
Western Gnatcatcher		x	x		
Western Ruby-crowned Kinglet					N N
Shrike	x	x x	x		
Plumbeous Vireo		x x	x x	x	
Western Warbling Vireo				xYx N	xNx
Virginia's Warbler				x x	
Audubon's Warbler				N	N N
Black-throated Gray Warbler		Y Y	x x		
Grace's Warbler				x Y x	
Macgillivray's Warbler				x	x
Cowbird	x	x	x		
Western Tanager			x	x x x	x x x
Rocky Mountain Grosbeak		Y	x x		
Lazuli Bunting	x	x	x		
Western Evening Grosbeak					N Y
*Cassin's Purple Finch					N
*Pine Grosbeak				x	
*Pine Siskin				x x x	N
Pale Goldfinch					x
Green-backed Goldfinch	x	x x	x		
*Crossbill				x x	x x x
Green-tailed Towhee	x	x x	x x x		
*Spurred Towhee		x		x	
Western Vesper Sparrow		x			
Western Lark Sparrow	N	x	x		
Desert Sparrow	x				
Northern Sage Sparrow	x				
*Red-backed Junco				x	N N
Western Chipping Sparrow		N	N	N	N
Brewer's Sparrow	N	x			
White-crowned Sparrow					x N x x
*Mountain Song Sparrow				x	x

2. The *Pinus brachyptera-Sciurus kaibabensis* association of the montane forest climax
3. The *Picea-Abies-Sciurus fremonti* association of the montane forest climax
4. The *Stipa-Carex-Thomomys* associes or mountain grassland.

Adjacent to the plateau are extensive areas of short-grass grasslands, both on the east and west, Basin sagebrush toward the north and northwest, and canyon desert scrub in the canyons bordering the plateau on the south and southwest.

VI. THE WOODLAND CLIMAX

THE *Pinus-Juniperus-Neotoma* ASSOCIATION

GENERAL

The piñon-juniper woodland forms a characteristic association, arranged as a belt below the yellow pine forest, throughout the southern Rocky Mountains. It attains its greatest areas in Utah, Colorado, Nevada, Arizona, and New Mexico. Only a few areas are

FIG. 9. Characteristic view of the woodland climax (*Pinus-Juniperus-Neotoma* Association).

found north of latitude 44° (Fig. 9). On the Kaibab Plateau this belt is usually found between 5,500 and 6,800 feet (1,675 and 2,075 m.). There is the usual extension of the upper limits on exposed southwestern slopes, occurring often up to 7,250 feet (2,200 m.), and the downward extension on the cool north and northeastern slopes where the upper limits may be 6,500 feet (1,980 m.), the lower limits as far down as 5,000 feet (1,525 m.).

In this woodland or "pigmy forest" the trees do not ordinarily form solid stands, but are scattered with intervening spaces of grass, sage or other shrubs, depending upon location. The trees do not usually attain a height of more than twenty to thirty feet (6-9 m.). They branch from near the ground and are very often nearly as broad as tall. Only in the bottom of draws and toward the upper limit of the association do the trees grow closely enough together to cast a continuous shade.

Throughout the Great Basin and adjacent areas trees of this woodland are usually intermingled with

sagebrush, *Artemisia tridentata.* The sage occupies the more level ground with deep soil and the piñon-juniper occurs on shallow rocky soils and rough, broken country.

On the Kaibab Plateau this association has its greatest width on the north, west, and east slopes, where it varies from four to twelve miles (6-19 km.). Along the south it is confined mainly to the upper slopes within the Grand Canyon and the lower and more exposed portions of the rim. The association is isolated from similar vegetation with exception of the extreme northeast end, where there is a slight break and the same type exists to the northeast. This association fragment covers an area of 435,000 acres (176,000 ha.).

The two stations selected for study in this community were similar in taxonomic composition and appearance, but one, A, was near the north end of the plateau, located on the top of a flat north-south ridge in Section 30, Township 39 N, Range 1 E at 6,000 feet (1,830 m.) elevation; while the second, B, was located towards the western side of the plateau on top of a flat east-west ridge in Section 35, Township 37 N, Range 2 W, at 5,800 feet (1,770 m.) elevation. Their greatest observable difference was that station B and its vicinity had been severely overbrowsed by the deer, while station A was only slightly browsed by them.

VEGETATION

The dominant plants are the two trees, the piñon, *Pinus edulis,* and cedar or juniper, *Juniperus utahensis.* These occur in a fairly even ratio over large areas. The piñon, however, reached its maximum development at a slightly higher elevation than the juniper. Near the upper limits of the association these characteristic trees become less abundant, but of good size, and then gradually give way to the first of the yellow pine. Some local areas have a narrow portion of Petran chaparral, oak-brush climax, forming a belt between the two major forest communities.

Considerable variation is shown in the vegetation of the understory in this association. Blue grama grass, *Bouteloua gracilis,* is the most abundant and widespread of the plants, forming in many places practically the only other abundant plant besides the dominant trees. It attains its greatest abundance in the lower half of the association. This is especially true of the eastern borders, where the piñon-juniper is bordered by an area of grassland, in which *B. gracilis* is the dominant plant. This relationship differs from the distribution of the same species in the region near Flagstaff, Arizona, where Hanson ('24) reports "*B. gracilis* was near its limit of xerophytism in the lower part of this (piñon-juniper) association." Towards the north the most important dominant is sagebrush. Finger-like projections extend up into the piñon-juniper community from the plains below. The sagebrush is gradually replaced until it is practically absent at the upper limits of the community.

Cliffrose, *Cowania stansburiana,* is abundant and generally distributed throughout the association. Although ordinarily a shrub, showing considerable branching and spreading, and growing from five to ten feet high (1.5-3 m.), it is not uncommon on the Kaibab for it to form small trees from fifteen to twenty feet (4.6-6.1 m.) in height. There is some extension of this species into the yellow pine, but maximum development is in the piñon-juniper. It is of extreme importance because it is the most important single winter deer food. Some areas have not been damaged by severe browsing. Others, for example, on Sowats Points at the extreme western edge, where Cowania was the most abundant of all the shrubs and trees, have been so badly overbrowsed that at the time of study only 10 to 20 percent of these plants had survived, and most of the growing portions of these individuals were beyond the reach of the deer (Fig. 10).

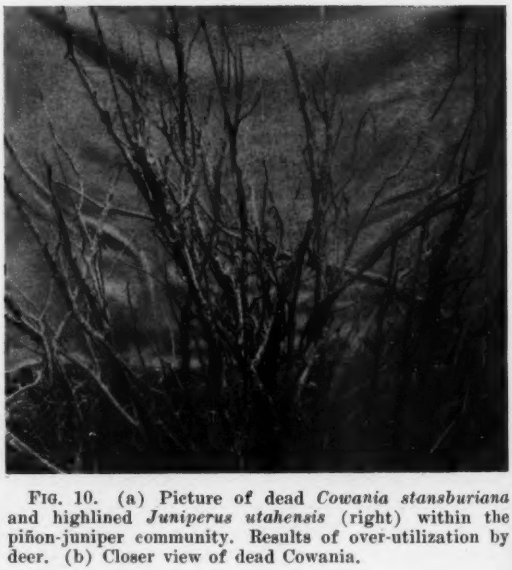

FIG. 10. (a) Picture of dead *Cowania stansburiana* and highlined *Juniperus utahensis* (right) within the piñon-juniper community. Results of over-utilization by deer. (b) Closer view of dead Cowania.

Subdominant shrubs of general occurrence are: *Amelanchier alnifolia, Quercus utahensis, Ephedra viridis, Yucca baccata,* and *Chrysothamnus* sp.

Subdominant shrubs of local importance are: *Purshia tridentata, Cercocarpus ledifolius, Artemisia nova, Fallugia paradoxa, Coleogyne ramosissima, Quercus turbinella, Atriplex confertifolia, Opuntia basilaris,* and *Forsellesia* sp.

Subdominant herbs and grasses are: *Gilia, Artemisia mexicana, Solidago petradoria, Pentstemon* spp., *Calochortus nuttallii, Sphaeralcea marginata, Oreocarya* sp., *Hymenopappus lugens, Erodium cicutarium, Oryzopsis hymenoides,* and *Sporobolus* sp.

Table 4 gives sample counts showing number of the larger plants per 1/20 acre (1/50 ha.), on basis of sample plots in the lower, middle and upper portions of the association. The counts were made near station A at the northern end of the plateau.

TABLE 4. Showing the number of larger plants per 1/20 acre (1/50 ha) within the piñon-juniper woodland. Sample plots located near the lower middle and upper portions of the community. Percentage of cover refers to estimated amount of herbaceous cover on the ground.

	Lower	*Middle*	*Upper*
Pinus edulis	9	15	8
Juniperus utahensis	11	10	6
Cowania stansburiana	3	7	11
Ephedra viridis	4	0	0
Odostemon fremontii	1	0	0
Opuntia acanthocarpa	1	0	0
Opuntia basilaris ?	4	1	0
Yucca baccata	1	4	0
Artemisia tridentata	67	16	7
Echinocereus coccineus	1	1	0
Amelanchier alnifolia ?	0	2	4
Quercus utahensis	0	1	13
Gutierrezia sarothrae	5% cover	20% cover	10% cover
Bouteloua gracilis	30% cover	10% cover	5% cover

MAMMALS

The native mammals of major importance, major influents, within the piñon-juniper formation are limited only rarely to this definite plant community in their year-long and breeding distribution. They are the Rocky Mountain Mule Deer, Mountain Lion, Mountain Coyote, and Plateau Bobcat. Figure 7 shows the distributions of more common vertebrates on the area.

The most important animal of herbivorous habits, and the animal the region is famous for, is the Rocky Mountain Mule Deer. All parts of the plateau are visited by this animal, and during the three years of intensive study the numbers of deer on the plateau were estimated at: 1929, 30,000; 1930, 25,000; and 1931, 20,000.

The entire herd spends the winter and shows greatest concentration of the year within the piñon-juniper association. The peculiarities of homing habit or unknown stimuli during the fall migration cause the deer to return year after year to certain favorite localities. They fail to distribute themselves evenly over the desirable range. The result is that some of these localities are nearly destitute of suitable food, while other areas available, but out of the main line of drift, have an abundance of food and are hardly touched. This is in agreement with Clepper ('31, p. 21) who says of the white-tailed deer, found in Pennsylvania, "They are very loath to seek out new feeding grounds. . . . Will remain and live in . . . region on a starvation diet rather than seek out new feeding areas even within a few miles of their home range." And it is in disagreement with Russell ('32, p. 39), who in speaking of the western mule deer, says, "Availability of desirable food is the most important controlling factor in determining range to be occupied by deer at all times."

Deer on the Kaibab Plateau scatter with considerable extension of range to seldom used areas in the late fall and early winter. Later, however, migrations to the concentrated regions take place with all but a few individuals, even from seemingly more desirable areas. The presence of food does not explain the difference, nor does any other obvious reason. The activity, however, is the same year after year.

The deer start entering the piñon-juniper in late September, and by late October a large percentage has usually migrated. In this downward movement there are well-defined migration routes or drift trails, which are very evident following early winter snowstorms. Migrating deer find shelter during severe storms and move as the storm clears or lessens. After an early heavy snowstorm the entire herd goes down on the winter range and subsequent storms will hold it there. However, if the weather clears up, there may be considerable upward movement again until the country becomes entirely snowbound. In spring the upward movement follows closely the clearing of the ground of snow and the availability of forage plants above the piñon-juniper. The majority of animals leave the piñon-juniper within a few days. On the west side of the Kaibab this movement averages near the fifteenth to the twenty-fifth of April.

Censuses of deer numbers were made by riding over winter range and actually counting individuals on sample areas and estimating the total numbers on the basis of area covered. Systematic winter counts to determine total deer numbers on the Kaibab were inaugurated in February, 1930, and have been continued since that time. A count made in February, 1931, by representatives of the United States Forest Service and Park Service, the Arizona State Game Department, and the author, resulted in the actual counting of 2,700 head. A sample area count was made the afternoon of February 23, 1931, in what is called the "Jump-up Pasture," a broad point extending toward Kanab Creek, with an area of 5,000 acres (2,000 ha.). It is bounded by perpendicular cliffs of several hundred feet, except at the north end, which joins the plateau proper. Eight riders counted 436 deer of various ages on this area

or one deer per 11.5 acres (4.65 ha.). This was believed to represent near two thirds of all deer on the area. Assuming that the count represented 66.6%, there was a population of 654 deer or one deer per 7.6 acres (3.1 ha.) or 84 deer per section. This is not an unreasonable estimate if one judges the efficiency of careful range counts of cattle in the southwest. Usually such counts show only 75 to 85 percent of the animals that are secured in the drive-off in the fall.

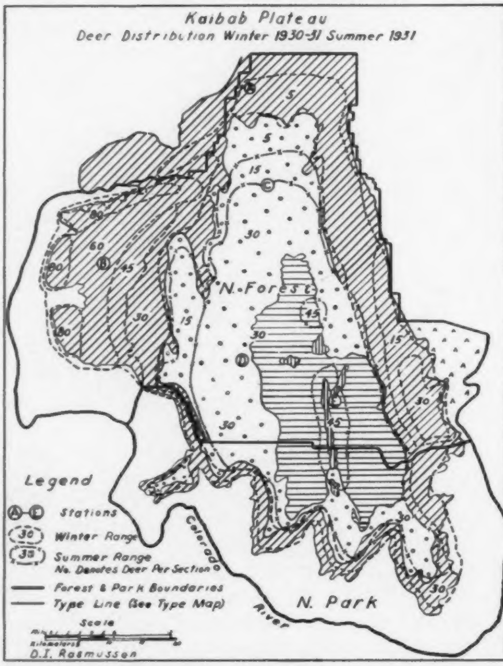

FIG. 11. Numbers and distribution of mule deer on Kaibab Plateau, Arizona. Winter 1930-1931, summer 1931. Numbers within regular broken lines signify numbers per section (640 acres, 260 hectares) in late winter. Numbers within lines broken by crosses signify numbers per section in midsummer. Types are same as on type map, Figure 2.

Figure 11 shows the late winter and mid-summer distribution of deer on the plateau. For the most preferred west-side winter range this figure shows the concentration is approximately 8 acres (3.24 ha.) per deer or 80 deer per section. On the average winter range there are 45 to 60 deer per section or 11.7 to 14.2 acres (4.7 to 5.75 ha.) per deer. In the past the concentration over the entire area is believed to have been four to five times as great.

On the basis of the condition of the vegetation and presence of remains of dead deer it is estimated that at the peak, deer numbers were as abundant as one per acre over several thousand acres of very productive winter range on the points bordering Kanab Creek. This resulted in killing out or "high-lining" of nearly all available forage, including the unpalatable species, such as piñon pine. On winters following this severe use there was only 5-10 percent as much forage available for deer as on similar but unbrowsed or moderately browsed areas. Marked reduction in winter carrying capacities occurred over all of the heavily used areas, although not as severe as on the above-mentioned area.

The area of the northern end of the plateau and along the eastern border to Kane supports a few deer. Late winter investigations showed that there were about five or fewer deer per section, or 128 acres (52 ha.) per deer. In the late fall and early winter (Oct. 1-Jan. 1) the area often supports three to four times this number.

A concentration area is present on the east side of the plateau in the neighborhood of South Canyon and the north slope of Saddle Mountain. This is of interest in the history of the Kaibab deer, because on December 16, 1924, a small area of this range was to furnish not less than 3,000 or more than 8,000 head of deer for the celebrated deer drive across the Colorado River, these to be delivered at the south rim of the Grand Canyon at the cost of $2.50 per deer. At that time deer were extremely abundant and many thousands were observed ahead of the 125 whites and Indians who were to act as drivers at the beginning of the so-called drive, but these were all back of them at the finish. In the winter of 1930-31 deer were not nearly as numerous on the east side as on the western border of the plateau. The maximum east-side winter concentration in 1931 was about 30 deer per section. On this east-side area the die-off of deer was even more complete, and the peak preceded the great mortality on the west side by a year. The east-side range has recovered from the severe damage of several years ago, and the 1931 deer numbers were not in excess of the grazing capacity.

The remaining portion of the piñon-juniper consists of a relatively very narrow strip along under the rim of Grand Canyon. The unevenness of the rim itself, with all canyons and points, greatly increases the length of this strip. The distance along the rim, including the rim of Powell's Plateau, from Saddle Mountain to Big Saddle above the Crazy Jug, is approximately 100 miles (161 km.). Deer from the top of the plateau move over the rim in small numbers all the way along. There is concentration in the neighborhood of Point Sublime and Powell's Plateau, with resulting heavy damage to browse there. It is impractical to count the numbers of deer occupying this strip of country, and estimates must be very general. There is an estimated 1,500 to 2,000 head during the winter of 1930-31 along this entire strip. This area is within the Grand Canyon National Park. The decrease in number of deer in the past years on certain areas, notably Point Sublime and Powell's Plateau, has been similar to that of those within the National Forest.

In the piñon-juniper woodland the deer show considerable choice of forage plants. They have some

very definite choice species, but do not feed entirely on any one species for even a day. Browse makes up the bulk of the food, and cliffrose, *Cowania stansburiana*, juniper, *Juniperus utahensis*, and sagebrush, *Artemisia tridentata*, are the main browse plants that are utilized. Figure 18 shows the year-long food habits of the mule deer and gives comparative amounts of the various species eaten at the time of this study.

The deer influence the community by browsing on a great majority of plant species present. A reasonable number of deer fit into the biotic make-up of the association without greatly hindering the growth or favoring the increase of any one species. It is even believed that browsing stimulates growth of certain species and that shrubs may produce more growth if browsed moderately than if totally protected. Such an example is given for Cowania on the Kaibab by Dayton ('31). Examination of such plants in the field, however, shows that those portions of the plant showing increased amount of growth as a result of browsing do not produce seed.

The excessive numbers of deer have thinned out the shrubbery and favored the growth of certain grasses and herbs which they do not usually select as food. These plants are favored by the increase of space and the decrease of shade and root competition. In certain Kaibab areas the whole aspect of the range is changed by a decrease in shrub species and increase in grasses resulting from deer usage. It is even logical, on the basis of the observable facts, to see where it would be possible for deer to turn a woodland containing abundant browse into an area resembling a savannah and by continuous use hold an area in a subclimax state.

The cougar, mountain lion, puma, or panther, as it is variously called, is known in the territory of the Kaibab Plateau simply as "lion." This region has long been famous as a lion country, which implies that lions are fairly numerous and generally distributed. But even when abundant, they are very rarely seen except when trapped or hunted with dogs. The number present in former times is impossible to ascertain due to their secretive habits. The number that has been removed is startling, and yet there is a good representation left at the present time. Forest Supervisor Mann has made a careful check-up on records of past removals. Previous to 1931, 781 were taken. "Uncle Jim" Owens, the pioneer in the hunting of mountain lions with dogs, claims to have killed or captured at least 600 from 1906 to 1918 on the Kaibab (Mann and Locke, '31). Since 1923, when the last federal government hunter was employed in the Kaibab, hunting of lions has been for sport and trophies under special permits.

During the study period the total lion population on the plateau, which includes the National Park and the National Forest north of the canyon, is estimated as fifty individuals. The range of these animals is limited and quite definite, and even with the great amount of hunting, certain comparatively small areas are and always have been good lion country. The lions limit themselves in the main to the canyon rim, where they have a safe retreat and yet are near locations where deer are found. Only occasionally are individuals found up on top of the plateau. Past reports seem to show this always to have been the condition.

They are primarily deer-eaters, and their pressure on a herd of deer is enormous. Grinnell ('24) estimates that a mountain lion kills a deer a week within the region of the Yosemite. In addition to personal observations, interviews gave further information on this subject. "Uncle Jim" Owens, in 1930, after tracing down over 600 lions mostly on the Kaibab Plateau, said very definitely that the "lion feeds on a fresh kill of deer, colt, or calf, as the case may be, three times a week." Jack Butler, interviewed in the years 1929, 1930, and 1931, is a trapper and guide and an extremely careful observer. He has captured over 150 lions on the Kaibab and believes that each adult Kaibab lion averages two deer every week. Butler trails the lions with dogs, and thus locates all kills that a lion has made or visited. He also reports examples of one lion's tracks leading to two kills both less than a day old. Maximum kills by lions could certainly be expected under conditions of deer abundance similar to those existing on the Kaibab.

Lion kills were located throughout the period of the field study and were easily identified. Usually the lion had devoured all the flesh and organs except the paunch and the digestive tract. In those kills that had been only partially eaten, the viscera had, as a rule, been taken. A lion may or may not return to its kill to feed again, regardless of the fact that it usually covers the carcass with needles, limbs, or even rocks.

No evidence was found of lions utilizing any appreciable numbers of smaller rodents or birds. This, no doubt, happens, but not to any great extent on this area. The professional lion-hunters of the plateau are sure that the smaller vertebrates contribute very little to the animal's total diet. They do occasionally kill and eat porcupines in this area. Young horses are killed and eaten, and local cowboys say it is nearly impossible for either a tame or wild mare to raise a colt near the lion areas. One valuable horse weighing 800 pounds (365 kg.) was killed by lions near Powell's Plateau during the summer of 1930.

In the examination of numerous kills and reports of many others there was no evidence recognized that the deer killed by lions represented anything other than a cross-section of the adult herd of the areas the lion hunted. There appeared to be some preference shown for mature bucks, but this could be indicative of the areas the lions hunted.

The mountain lions are found with the piñon-juniper during the period when the deer are present. In late winter tracks and "kills" were found in various parts of the community. These were usually

within local areas that are recognized as lion country. One well-defined area of some 70 square miles (180 km.^{2}), including South Canyon on the eastern edge of the plateau and containing a great amount of rough country, cliffs, and ledges, supports 8 to 10 lions. According to best available information, the number here has never been in great excess of this. Butler reported knowing of two litters of kittens in this area in the summer of 1931, but believes them to be the only new ones during the year. When lions are hunted out of this area, as has been done several times in the past, other lions are definitely known to have moved in from the outside.

The cougar has a very definite place in the biotic relations of the piñon-juniper community, if by its abundance and its pressure on deer, deer numbers are influenced. As herbivores, the deer exercise the greatest direct influence on the native plant species of the woodland association and apparently influence, directly or indirectly, the majority of organisms present.

During the period of study the coyote was as abundant over the Kaibab as in any time in the past, and apparently had increased in recent years in spite of consistent trapping. Coyotes are present within the piñon-juniper throughout the year. The summer population is the lowest per township (23,040 acres; 9,325 ha.), estimated at 20 to 25 as compared to 30 to 40 per township in the higher portions of the plateau. In the fall, there is a considerable downward movement of the coyote population and a marked increase during the winter in this community. This is true of areas of deer abundance as well as areas where deer are scarce or lacking.

In the late fall of 1931 several individuals could be seen by close observations during one day's ride. Tracks and droppings were in evidence in great numbers and numerous individuals were heard. A series of coyote droppings collected in mid-winter showed primarily deer hair and bones with some rabbit fur, remains of Peromyscus and a small amount of grass. Another series of droppings from late summer consisted primarily of vegetable matter, juniper berries, service berries, prickly pears, grass, and rodent remains. Within this community the coyote's main year-long food is the small rodents that are found here.

During the time deer are present, there is use of them as food, but hair in the droppings and evidence of their having eaten deer does not of necessity mean the coyote is responsible for killing. In February 1931, however, many dead deer were found, and a great number had not been disturbed by carnivores; while numerous others showed definite evidence of having been killed by coyotes. A preference for meat of its own killing or freshly killed meat, was clearly indicated.

The generally conceded increase in coyote numbers on the plateau has possibly been affected by an increased supply of weak and dead deer available in the mid-winter, normally a season of food scarcity. However, evidence also points to an increase in coyote numbers following extermination of the wolves.

It is estimated that there was a total 1931 coyote population of 1,000 animals. Trapping in recent years has been done almost entirely in winter for the fur, with an average annual removal of two to three hundred animals. A small amount of poison for coyote control was placed out on the plateau in October 1925. A number of coyotes and some valuable dogs were destroyed. No poison had been used previously nor has it been used since that time.

The plateau wildcat or bobcat is a fairly common resident of the association. Its nocturnal and retiring habits do not make its presence very obvious. In suitable habitats its round, small tracks are usually in evidence. Its breeding distribution is local and it often is confined to areas of cliffs and ledges. It is distributed entirely around the edge of the plateau, and reaches its greatest numbers in this association and in the lower portions of the yellow pine. In total numbers it does not equal the coyote, estimates of numbers for the plateau and surrounding canyons being near 500.

Its food consists primarily of small rodents and some birds. Bobcats perhaps take some fawns, but exact evidence is scarce. They have no trouble in killing sheep and are accused of taking heavy toll of lambs in the near-by region.

Its usual residence is in what is also the favorite haunts of certain white-footed mice, the woodrat, and cottontail rabbits. These rodents are eaten by the bobcats and are believed to constitute the bulk of its food. Its outstanding influence takes the form of pressure on the rodent population.

Influent mammals of this community are the:

Kaibab Woodrat	Black Hills Cottontail
True's White-footed Mouse	Utah Rock Squirrel
Tawny White-footed Mouse	Yellow-haired Porcupine
Utah Cliff Chipmunk	Arizona Gray Fox
Jack Rabbit	

The Kaibab woodrat is characteristic of the piñon-juniper distribution, and is fairly common over the area. It makes use of cliffs and rocky slopes when such are available, but is also distributed where these conditions are not present. Here the characteristic nest may be placed about the stump of a juniper or piñon, under the protection of the spiny leaves of yucca or in a rocky outcropping. One was found occupying the shelter provided by the dry hide of a dead cow, as it remained stretched over the skeleton. The nests are made up of all that a "pack rat" collects.

A pack rat nest near Slide Reservoir, examined October 1931, was taken apart following the trapping of the occupant. The record of material was as follows: bulk approximately ten bushels (350 liters); 85% sticks and twigs of piñon, juniper, and holly-grape, and some miscellaneous plant species; 5% empty piñon cones; 4% a great variety of bones of cattle, horse, deer, rabbit; 2% rocks; 1% cactus (Opuntia); 1% mushrooms; and 2% deer hide and

hair. The deer hair was plentiful throughout the nest. The nest also contained about one-half pound (225 grams) of piñon nuts, and a small collection of juniper and hollygrape berries.

It seems that this animal is well adapted in habits of living and food relation in this association. It has a wide range in choice of foods. Among those usually taken is the piñon nut, which it stores in great quantities during years when they are abundant. It is fond of juniper berries, fruits and seeds of a variety of plants, herbaceous growth in summer, and in winter it was observed to have eaten considerable quantity of the heavy leaves of *Yucca baccata*.

Some careful area counts were made. In level portions of the piñon-juniper the occupied houses were estimated to be one per one and one-fourth acre (two per ha.). As a rule a single rat was found in a nest. They are active throughout the year and although they store foods, they use these materials only in supplementing what they obtain by foraging about.

True's white-footed mouse is perhaps the most abundant mammal species within the piñon-juniper. They are most common in regions where cliffs and broken country provide suitable breeding localities. They are not limited to such areas, and mice droppings are seen about hollow stumps and fallen trees of piñon and juniper throughout the woodland. They are strictly nocturnal and were present wherever camp was made or traps were set among piñons and juniper. They are found in the same localities and mingle with the tawny white-footed mouse. Because of this their food habits are difficult to determine specifically. Their appetite for grain of all kinds is very marked. In natural conditions juniper berries, grass, and herb seeds appear to be the main diet. They are two or three times more abundant at this lower elevation than is the tawny species.

Estimation of area populations of mice are difficult to determine. The seasonal difference is perhaps over 200 percent, and the entire population is subject to periods of great abundance following favorable conditions. Mice in general appeared to be more abundant in this community than in others studied. These mice are active all year although the main breeding season is believed to be early summer. A female containing four embryos was taken in October, 1931. An estimate of twelve to fifteen Peromyscus per acre was made on the basis of trapping a series of measured areas (October, 1931).

The cliff chipmunk is present throughout the community, but is another species preferring a habitat consisting of cliffs and ledges. They are not as abundant as the chipmunks of the upper forests, but are seen wherever desirable habitat conditions exist. They are very adept at climbing cliffs and trees and feed upon a variety of available foods—piñon nuts, juniper berries, acorns, fruit of the cactus, and seeds of composites. They are active almost year-long, with some inactivity during more severe weather, when they are dependent on their stores of food.

The blacktailed jack rabbit is abundant in the area surrounding the Kaibab Plateau, and extends upward with the sagebrush through the piñon-juniper to the yellow pine. It is a very characteristic mammal of the western deserts and semi-deserts, and ranges over a number of plant communities. It is abundant enough in the area to have considerable influence on the association because of its voracious feeding habits. Vorhies and Taylor ('33) have shown in the closely related species, *Lepus californicus eremicus* (Allen), that 12 rabbits ordinarily eat as much as one sheep. There is some difference in their distribution, according to the amount of sagebrush present. This is interesting in view of the fact that this rabbit's diet on the study area was primarily grass, but presence of sage limits distribution.

At study stations A and B the rabbit populations were very similar, although a few more were present at B, the heavily grazed area. The three years, 1929-30-31, showed no great variations in numbers that were obvious in general census. In this area there has been no conspicuous peak of abundance or scarcity within the past decade. Where conditions were favorable for the species, repeated counts of rabbits showed a population of one per ten acres (4 ha.). Over the entire association the average would be nearly one rabbit per twenty-five acres (ten ha.). This is much lower density than in the near-by sagebrush desert.

The cottontail rabbit is found throughout the association in small numbers, but is not so abundant as the jack rabbit. It is ordinarily seen in the local situation of brush slopes.

The rock squirrel is local in distribution according to the rocks and canyon walls, but is most abundant at the upper edge of the piñon-juniper, oak brush, and steep, rocky hillsides, where there are often several per acre. Under the rim of Grand Canyon they range upward to 8,000 feet (2,440 m.) on the exposed rocky sides, which support a growth of scrub oaks and similar vegetation.

The porcupine is found in small numbers in this association. There appeared to be an increase in numbers during fall and winter. Individuals, droppings, and tracks were observed that would indicate a limited downward migration from higher elevations in this season. The piñon is their main food in this community, but some Cowania showed evidence of porcupine attack. They are rare and show no uniformity in distribution.

Three mammals of minor influence, mainly because of the scarcity of numbers, but found in this association are the gray fox, ringtailed cat, and the little spotted skunk. Several fox are trapped each year, but nowhere is it abundant enough to be of great ecologic importance. This animal ranges below the piñon-juniper and is occasionally trapped in the rougher, lower country. It is usually an animal of the broken foothills.

The ringtailed cat is limited in distribution by canyon walls and ledges, but is occasionally encountered by tracks or trapping. They range above and below

the association where suitable localities occur. They are never very abundant and four or five has usually been the annual catch on the plateau.

The skunk occurs in small numbers within the Grand Canyon. The absence of streams on the summit of the Kaibab appears to be a factor influencing their rareness. Occasionally one is found on the plateau, two were trapped at the upper limits of the piñon-juniper near Big Springs Ranger Station in 1931.

Birds

The birds of this association are more abundant per unit area of climax woodland than in the true, unbroken climax of any other major association on the Kaibab. (The greatest bird concentration of the plateau, however, is along the park and meadow boundaries of the higher elevations.) The seasonal and stratal societies of birds and invertebrates are well defined. The stratification is not as conspicuous as in other forest associations due to the very scattered arrangement of the dominant trees, which usually do not exceed 15 to 20 feet (4.6 to 6.1 m.) in height.

Counts of breeding pairs of birds by repeated counts of singing males during May, 1931, showed as many as eight birds on five acres (2 ha.). The large number of birds on this area is surprising because it is usually three to five miles (4.8 to 8.0 km.) air-line to the nearest permanent water, and because in late May and June this association very often lacks any measurable amount of precipitation. The scarcity of water and absence of subclimax vegetational stages are believed to be the cause of absence of a number of birds often listed as the commonest species at comparable elevations near-by.

Most abundant resident birds are:

Gray Titmouse	Red-shafted Flicker
Woodhouse's Jay	Piñon Jay
Western Red-tailed Hawk	Lead-colored Bush-tit
Golden Eagle	Rock Wren

The gray titmouse is limited practically year-long to this association, being the least migratory of the native species. It forages about the smaller limbs and twigs of trees and larger shrubs. Observations in the field proved that the abundant leaf-hoppers were eaten in great numbers in summer, along with a large assortment of other small forms. In winter, when no insects are active, they continued to forage in the same niche; the food then must, of necessity, be mainly dormant insects. They utilize plant material to some extent, but the relative percentage is unknown.

The Woodhouse's jay is also present year-long in this association and the oak brush belt. There is some movement to lower country in colder weather. This jay's food is a combination of vegetable and animal material. It forages in general over all strata, a considerable portion of its food being collected from the ground.

The western red-tailed hawk, although present over the entire plateau, is of influence here because of its year-long residence. In summer it is not abundant, there being only one pair per section. In winter this number is doubled. Its soaring habits make it conspicuous at all times. The jack rabbits, cottontails, and mice appear to be its main winter foods. This is varied with other rodents in summer.

The golden eagle nests and is present year-long in the rough, rugged country that abounds all about the plateau. In summer it is occasionally seen well up on the higher elevations, but is usually in the rocky box canyons to the south and west. It is seen foraging over the level country ten to twenty miles (16 to 32 km.) back from the canyon. In winter there is a decided upward movement and numbers are seen on the plateau. It is not adverse to the use of dead deer, and in past winters these have provided easy food. This has resulted in a great influx of golden eagles to the west portions of the Kaibab each winter. One reliable observer counted eighteen of these large birds in a limited area, December, 1929. This is unusual, but individuals are usually present in some numbers throughout the range.

The red-shafted flicker appears in all wooded portions of the plateau. The abundant ants provide the bulk of their food in open seasons. There is a downward migration in the fall and an increase of their numbers in the piñon-juniper during winter.

The piñon jay occurs very irregularly according to the success of the piñon nut crop, which is very indefinite and spasmodic. Flocks are often seen. They were abundant in the fall of 1931, the time at which the Kaibab had its first good piñon crop in three years.

The lead-colored bush-tit is present. Flocks of this diminutive bird are seen in this association, but not elsewhere.

The rock wren ranges throughout the association with a very marked preference for the exposed rocky slopes and ridges.

Open season or summer resident birds of importance are:

Western Chipping Sparrow	Night Hawk
Black-throated Gray Warbler	Northern Cliff Swallow
	Western Lark Sparrow
Rocky Mountain Grosbeak	Desert Sparrow
Western Mourning Dove	

The western chipping sparrow is found in all parts of the plateau, except in the deep forests of yellow pine and spruce-fir. It usually occurs along borders of woods and more open portions. In the piñon-juniper this type of niche is common throughout the climax, due to its open orchard-like arrangement, and the chipping sparrow is found throughout the area. In numbers it is the most abundant bird during the time it is present in this association. It usually forages on the ground; and although a sparrow, it has been shown that animal matter makes up sixty-two percent of its food (Bailey, '28).

The black-throated gray warbler is a common bird that occurs throughout the community but they are less abundant nearer the lower limits. They forage in the crowns and mid-branches of the trees, and individuals are rarely seen on or near the ground. The Rocky Mountain grosbeak is a very characteristic and common bird of this community.

Other abundant open season birds are the western mourning dove, which occurs commonly but is limited by distance from water; the night hawk, which is seen regularly throughout the association, its activity being confined to evening, night, and early morning; and the northern cliff swallow, which occurs locally according to available nesting sites.

At the lower edges of the piñon-juniper, where there is considerable amounts of sagebrush, the very typical western lark sparrow, the desert sparrow, and an occasional sage thrasher occur.

The common winter resident birds are:

Shufeldt's Junco	Rocky Mountain Nuthatch
Pink-sided Junco	Mountain Bluebird
Gray-headed Junco	Western Robin
Red-backed Junco	Long-crested Jay

The most abundant birds found during the winter season in this association are the juncos. The red-backed junco, which breeds in the upper portions of the mountain, is present in winter along with Shufeldt's junco, with perhaps individuals of the pink-sided junco and the gray-headed junco. Flocks of juncos were observed in the snow-covered foothills in flocks of twenty-five to one hundred individuals in the winter of 1930-31. Both the "black heads" and the "gray heads" were present. The former exceeded the latter in numbers of three to one. They are active on the ground, and their food consists of all available plant seeds, grasses, herbs and shrubs.

The Rocky Mountain nuthatch is present year-long, but not in any great numbers. However, in fall and winter there is a downward migration, and solitary individuals were found throughout the piñon-juniper. In this association during mid-winter they forage almost entirely on the trunks and larger limbs, as they do on the spruces, firs and pines in summer.

Other more common winter residents include birds of the higher elevations—the mountain bluebird, the western robin, and at times considerable numbers of long-crested jays, which descend to this association from the montane forests above. During the winter the bluebird and robin also range lower than the piñon-juniper; the jay's distribution is limited by its lower border.

Reptiles

Reptiles found here are:

Short-horned Horned Toad	Western Collared Lizard
Sagebrush Swift	Great Basin Rattlesnake
Blue-bellied Lizard	Grand Canyon Rattlesnake
Brown-shouldered Uta	Great Basin Gopher Snake

The upper limits of the piñon-juniper mark the range in which reptiles are present in any numbers and have any marked influence on the community. One reptile, the horned toad, is found in small numbers in this association and becomes more abundant in the open yellow pine forests. This is the only reptile that occurs in any numbers above the piñon-juniper.

The sagebrush swift is the most common reptile, occurring up to the upper limits of the piñon-juniper. Some counts were made where it averaged six to eight per acre. Its food consists of terrestrial arthropods with a wide range of selection, ants being among those more often eaten because of their great abundance and accessibility. The two lizards, the blue-bellied and the brown-shouldered Uta, were both present in the lower and more open regions. The distribution of both species is local. The western collared lizard is present, but limited in its distribution to the rocky slopes and ledges, attaining its highest vertical distribution along the rim of the Grand Canyon.

The rattlesnakes are found in limited numbers along the rocky canyons extending upward from Kanab Creek and Grand Canyon and rarely on the rocky, exposed points.

The Great Basin gopher snake is found in the sagebrush and grassland regions at the base of the plateau, and individuals are found in the lower limits of the association, where the sage makes up a conspicuous part of the community.

Invertebrates

The invertebrate population was studied by regular quantitative collections. In this community the fifty sweeps of the shrubs included trees as well, and ratio of sweeps were: piñon eighteen, juniper sixteen, Cowania twelve, scrub oak two, and sage two. (This selection of plant species was based on the approximate amount of green vegetation of each species present at stations.) For the herbs the sweepings were practically limited to Gutierrezia and Bouteloua, the only abundant species.

The total population averaged about .20 million per acre (.50 million per ha.) and had its first maxima in the early estival period, late May, with a decline during the dry late estival period. A second lesser maxima was found in the serotinal period, following the rainy season. This second maxima was the result, primarily, of increase of the herb and ground strata population (Fig. 12).

Eighty-three species of invertebrates were collected quantitatively in this community; of these 37 were taken only once. Of the total number of individuals the groupings were as follows: 25% spiders, 13% Chermidae, 12% Formicidae, 8% other Hymenoptera (mostly Ichneumonidae), 10% Diptera, 9% Cicadellidae, 6% Hemiptera, 5% Coleoptera, 3% Orthoptera, and 9% others.

The most abundant invertebrates are the immature of the crab spider, ***Misumenops asperatus;*** the chermid, *Paratrioza cockerelli* (Sulc.); and the ant, *Formica fusca* var. *subaenescens*. All three were taken from tree-shrub and herb strata. The spider

and chermid were most abundant on the trees and shrubs. The ant was present in the ground collections as well. Complete names of Formicidae and Orthoptera are given in the appendix.

In the shrub and tree strata the following were most abundant species: immature spiders of genera Dendryphantes and Oxyopes; two leaf-hoppers, Cicadellidae; chermid, *Psyllia brevistigmata acuta* Crawford; a beetle of genus Anthonomus; and a fly of family Cecidomyiidae.

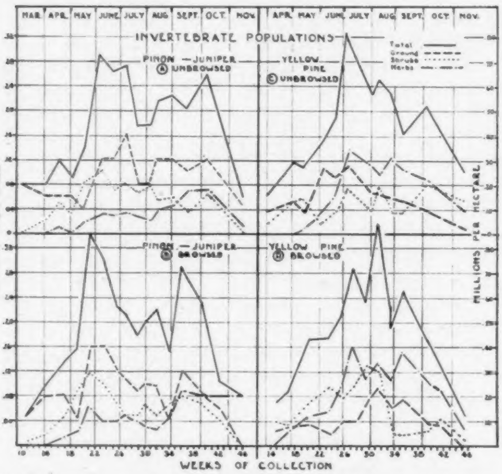

FIG. 12. Graph showing invertebrate population of four stations as indicated by quantitative collections made in 1931. A = Station A, unbrowsed area of piñon-juniper, north end of the plateau; B = Station B, area of piñon-juniper, heavily browsed, on west side of plateau; C = Station C, unbrowsed yellow pine, near Jacob's Lake; D = Station D, heavily browsed yellow pine, west side of the plateau.

In the herb strata the beetle *Monoxia* spp., found on the Gutierrezia, was the most abundant species. The banded-winged locusts, *Trimerotropis inconspicua*, *T. cincta*, and *T. cyaneipennis* were present. Their usual resting place was the bare ground in the spaces between the trees. They foraged, however, on both grasses and shrubs. In July, 1931, there was considerable local damage to cliffrose, sage, and grass on the western portion of the association by Orthoptera. This occurred in the area of greatest winter concentration of deer and most severely damaged deer range. *Trimerotropis cincta* was collected from Cowania as a possible causative agent.

On the ground surface ants predominated. In addition, the large black *F. fusca* var. *subaenescens*, as listed above, the *Leptothorax texanus*, and the very dark red *Myrmica scabrinodis* var. were found on vegetation and ground. The very small *Monomorium minimum*, and the odoriferous *Crematogaster lineolata* were found about fallen logs, tree trunks, and under rocks. Nests of *Camponotus maculatus vicinus* var. *luteangulus* were found under rocks, but no activity of this species was noted in midday. In the very open sites, most evident in sagebrush areas toward the lower parts of the association, were the mounds and individual burrows of the mound-building prairie ant, *Pogonomyrmex occidentalis*.

The termite, *Reticulitermes tumiceps* Banks, was found making galleries in both piñon and juniper wood, where dead limbs rested on the ground. The piñon seemed to be the favorite, however, and practically all pieces of any size were infested. A tenebrionid, *Eleodes* sp. and the carabid, *Cymindis blanda* Casey, were common. The poison spider, *Latrodectus mactans* (Fabricius) was found in the association under rocks on exposed ridges and was fairly common. An asilid, *Ospriocerus abdominalia* (Say), and a cicada, *Platypedia putnami* (Uhler) were characteristic species of this community.

The general collections did not show any great differences in insect infestation due to deer browsing. As a check for difference in insect infestation due to severe browsing, a separate series of collections were made. Two stations, A of a little browsed range and B of severely browsed range, were used. In addition, two other stations B_1 of moderately browsed but healthy shrubs, and B_2, an area of the most severe damage to the shrubs. These last two were also on the west-side winter range area, near Station B.

TABLE 5. Results of counts of invertebrates on 20 m.[2] (1,000 sweeps) taken over a period of four collections. May-June, 1931.

Station	Damage by Browsing	Total Insects	Total Insects per 20 m²
A	None	462	23.1
B	Severe	494	24.7
B_1	Moderate	552	27.6
B_2	Extreme	348	17.4
Average	....	464	23.2

The more abundant species were nearly the same at all four stations. The increase at station B_1 consisted primarily of Cicadellidae, Chermidae, and spiders. These groups were much less abundant at station B_2. There was a marked increase of insect numbers associated with the presence of a greater number and more compact arrangement of leafy shoots, a condition which results from moderate browsing in numerous shrubs. On the other extreme, where Cowania and juniper were low in vitality as a result of overbrowsing and had a minimum of shoots and new green vegetation, the number of insects were definitely less than average.

Further study of the species present will, no doubt, show some very definite changes in the species concerned, and very likely, an increase in the more important insects that attack the woody portions of the trees and shrubs, due to their weakened condition. The infestation of Orthoptera in July, 1931, was practically limited to severely browsed areas and was general over these areas. The damage was accentuated by the fact that the amount of new growth of browse here was only a fraction (estimated at

less than 10%) of the new growth present on slightly browsed areas.

Thus, an equal loss of vegetation on the two areas due to insect attack could be of minor importance with the normal plants, but very serious in the case of the heavily browsed areas.

The invertebrate population curves of the two stations within the piñon-juniper differ slightly (Fig. 12). The agreement in the main peaks and the ratio of animals of different strata to each other is marked. Station A is so located that seasonal changes are a little later than at station B. This is shown by the peak of abundance of invertebrates occurring slightly later at station A.

The total population reaches a higher peak on the severely browsed areas, but the difference in numbers is not great enough to be significant. The increase of animals of the herb strata of station B over animals of the same strata in unbrowsed plot of station A is the major difference. This is possibly due to the favoring of plants of herb strata where browsing has removed a great amount of the parts of shrubs and trees that shade the lower strata.

Invertebrate populations at both stations agree in their main characteristics, and the following conclusions can be drawn about the numbers of invertebrates in the piñon-juniper community that was studied:

(1) Ground stratum averages slightly more animals per acre than any other stratum.

(2) Shrub and tree strata average more per area than herb and grass strata.

(3) There are two maxima during the season, the first in late May and the second and lesser maximum in September.

(4) The total invertebrate population is much less than populations of deciduous forests of Illinois, as shown by studies of Smith ('28) and Weese ('24), or of aspen parkland, as shown by Bird ('29).

VII. THE MONTANE FOREST CLIMAX

THE *Pinus brachyptera-Sciurus kaibabensis* ASSOCIATION

GENERAL

The most extensive and typical true forest of western United States is that composed of yellow pine, *Pinus brachyptera* and *Pinus ponderosa* Doug. It is the most important economic tree of several southwestern states and occurs in pure stands in all far western states, in the Black Hills of South Dakota, in portions of western Canada, and in the mountains of Mexico.

The Kaibab Plateau has been greatly advertised because of its yellow pine forest, one of the nation's finest and largest undisturbed stands. On the plateau it is dominant between 6,800 and 8,200 feet (2,075 and 2,500 m.), extending downward to 6,500 feet (1,980 m.) on cold slopes and upward to 8,800 feet (2,680 m.) on certain exposed slopes and the canyon rim. It forms a belt of varying width about the plateau, being extremely narrow at the eastern border, but from eight to twelve miles (13 to 19 km.) wide at the west and north ends. The total area of yellow pine forest is approximately 245,000 acres (99,200 ha.). The summit of Powell's Plateau, an area of 2,500 acres (1,000 ha.) of this forest, is within the canyon and is separated from the main forest.

The forest itself is decidedly open. The trees are unusually large and mature, growing in groups or widely spaced so that the sunlight reaches the ground in almost all parts of the forest. The understory is usually free from shrubs or smaller trees and little fallen timber is present throughout the forest. The open nature is attested by the fact that one can drive a car for miles through the primitive forest. The limitations are matters of topography, not vegetation. This yellow pine forest is completely isolated from similar plant communities either by the Grand Canyon or twenty to thirty miles of piñon-juniper woodland and sagebrush.

The two stations selected in this community were similar in vegetational composition but differed in degree of browsing by deer (Fig. 2). Station C was located toward the northern end of the plateau, near Jacob's Lake Ranger Station, in Section 36, Township 38 N, Range 2 E, at 7,800 feet (2,380 m.) elevation. Here deer were often seen, but the vegetation was not damaged by them to any great degree. Station D was located a mile west of Dry Park Ranger Station, in Section 12, Township 35 N, Range 1 E, at 8,000 feet (2,440 m.) elevation. This is west of the highest portion of the plateau, in a region where deer at the time of study were extremely abundant during the summer, with increased numbers in the spring and fall. The range is very severely browsed, so much so that the seedling yellow pine are at a standstill because of deer pressure.

VEGETATION

The dominant plant is the western yellow pine, *Pinus brachyptera.* Other plants act as dominants in small areas but the climax consists of a pure stand of yellow pine (Fig. 13).

The trees range in size to over one hundred feet (30 m.) in height, and three to four feet (.9 to 1.2 m.) in diameter. Counts of trees on sample plots in the mature forest showed an average of only forty to fifty-five per acre with a d.b.h. of six inches and over. The younger trees occur regularly in small groups of similar age class, often 200 to 400 per acre.

With the exception of the yellow pine no tree or shrub occurs uniformly throughout the community in numbers that make it of great ecological importance. *Ceanothus fendleri* is a characteristic and quite uniformly distributed shrub, never having formed any very conspicuous part of the vegetation. It is more limited at the present time than previously due to the close browsing it has been subjected to by deer.

Robinia neomexicana is usually found in the lower portions of this community. It is rather common, often making up small stands among the yellow pine, and is frequently found in mixed patches with *Quercus utahensis.* For the entire forest the small and inconspicuous *Odostemon repens* is perhaps the most abundant shrub. *Arctostaphylos patula,* one of the very few shrubs unpalatable to the deer, occurs locally. This plant forms a conspicuous understory in the yellow pine on the Walhalla Plateau, at the extreme southeast portion of the plateau. Other shrubs that are found here are: *Chrysothamnus parryi, Sambucus caerulea, Ribes inebrians,* and *Sericotheca glabrescens.*

Symphoricarpos sp. occurs in upper portions of the community. Much of this species has been killed by the deer, and the remaining plants show that they have been closely clipped for years. Raspberry, *Rubus* sp., was formerly present and reported as common, but this species is now extremely rare. This is a known example of deer eliminating a desirable plant species; how many others have been destroyed in this manner is unknown.

At the lower border of the yellow pine association a number of trees and shrubs that are typical of the oak belt and of the piñon-juniper are often found growing under the yellow pine. *Quercus utahensis* is the most common shrub; it occurs as scattered individuals and makes up small colonies. *Cowania stansburiana* and *Amelanchier alnifolia* are abundant in certain localities. *Juniperus scopulorum, Pinus edulis,* and more rarely *Juniperus utahensis* occur as lone individuals or in small groupings in local situations. Hanson ('24) has shown that these shrubs and trees act as a seral stage in the primary xerosere of the yellow pine, and this appears to be the condition in the lower portions of the association of the Kaibab Plateau.

In the upper half of the community and extending downward in the cooler slopes and draws are stands of quaking aspen, *Populus aurea.* In the Southwest aspens are usually not present in any great numbers as low as the yellow pine. The aspen attains its maximum development above the yellow pine, but areas and scattered groups are present in many parts of the association. This species apparently forms a primary seral stage in the forest succession near the upper border of the community but it is also found in a variety of local situations.

In the greater portion of the forest the natural succession does not show a series of stages of tree or shrub species, and with the exception of changes

FIG. 13. (a) Typical scene in the montane forest climax (*Pinus brachyptera-Sciurus kaibabensis* Association). (b) Yellow pine bushy growth resulting from repeated heavy browsing by deer.

in herbaceous species the dominants are the same, yellow pine following yellow pine on areas of burns or "bug" kills.

The grasses, *Muhlenbergia montana, Blepharoneuron tricholepis,* and *Sitanion hystrix* are common herbaceous elements of the climax yellow pine forest. A conspicuous yellow Carex grows among the pine needles and directly under the trees throughout the community. A number of lupines are found here, a common one being *Lupinus barbiger.* Other common herbs are *Potentilla* sp., *Erigeron divergens, Solidago* sp., *Castilleja* sp., *Lotus wrightii, Artemisia gnaphalodes, Astragalus* spp., *Eriogonum* spp., and *Antennaria* sp.

The mistletoe, *Razoumofskya cryptopoda,* is parasitic on the yellow pine, usually forming conspicuous abnormal growths on the lower limbs of the mature trees. It is abundant throughout the forest, 10 to 20% of the older trees showing some sign of it. In some few cases death results from it.

Mammals

The major influents of this association are the same as the other forest communities of the plateau, namely the Mule Deer, Mountain Lion, and Mountain Coyote.

Although not a year-long resident in this association, the mule deer, due to its decided influence during the time it is present, is the most important animal species.

The major part of the deer herd enters this community in middle and late April. A number migrate on upward as conditions permit, reaching the summit and the regions of the mountain meadows at VT Park late in May. Thus during May the majority of the deer are in the yellow pine. During June, July, and August they are throughout the montane coniferous forest in both yellow pine and the spruce-fir communities. Again in September and October, depending to a great degree on weather conditions, the yellow pine is the area of maximum concentration of deer numbers.

There appears to be a segregation of sexes soon after the deer enter the montane forest, and this is evident throughout the summer. The bucks are in a majority at the upper and the extreme lower portions of the summer range; the does predominate in the intermediate region. Does without fawns act much as bucks do and are often associated with them. The bucks are sometimes seen singly, but are usually in small groups of two to five. The composition of these groups is not uniform, containing old, young, or both old and young animals. During fawning season, late June and early July, breeding does are most abundant in the upper portions of the yellow pine belt, where they are seen singly or in groups of two and three.

Summer population in the more concentrated areas amounts to 30 deer per section. For the entire yellow pine forest the average is near 20 to 30 per section (1931 data) (Fig. 11). The home range of a doe with a fawn or fawns seldom exceeds two miles (3.2 km.) in radius. It is believed that with abundant available water this would be much less. Does without fawns and bucks frequently range four or five miles (6.4 or 8.0 km.) from water. The extreme northern part, north of Jacob's Lake, has few deer during this season (5 per section, 1931).

The early spring migration follows so closely the melting of the snow that the growth of early herbaceous species is merely beginning when the deer first arrive in this community, and as a result the yellow pine is heavily utilized as food.

During the summer the deer feed mostly on the herbs and the few shrubs that are present, and eat only a small amount of yellow pine. In the fall an increase of the amount of yellow pine eaten is shown. From a standpoint of damage to the trees, the spring browsing is by far the most severe. Terminal buds and shoots are eaten, and the result is that the majority of the smaller trees within reach of the deer had made little growth for the decade preceding 1931. The leaders on these small trees within the fenced-enclosure plots that have been in existence for four and five years (1931) in areas of heavy deer damage show an annual growth of six to eleven inches (15 to 28 cm.), as compared with an inch or less for trees in the open.

Contrary to the general belief that the winter range is the only area of overbrowsing, examination of forage plants on the summer range shows this to be also severely damaged. The three choice summer browse species, Rubus, Symphoricarpos, and Ceanothus, have been greatly reduced in numbers and size of growth. No young aspens are present that are less than ten or fifteen years old (1931). Certain legumes are reported to have entirely disappeared. The blame for overgrazing of the herbaceous species should not be entirely attributed to deer, as the whole mountain has been subjected to severe overgrazing in the past by domestic livestock and wild horses. However, marked reduction of the browse species and the damage to the trees can be attributed primarily to the deer.

The maximum summer concentration of the mountain lion is in the yellow pine forest in those areas that are near the canyon rim or suitable rough country. They follow the deer herd in their migration, in and out of this community. The numbers, range, and peculiarities have been discussed under the animals of the piñon-juniper association.

Coyotes are present throughout the association year-long, their distribution is fairly uniform, with an estimated population in summer of 35 to 40 per township and only 10 to 15 per township in winter.

The downward movement of deer is a well-defined migration along certain main routes; whereas, in the case of the coyote, it is merely random descent, taking place all about the plateau, the intensity depending upon the severity of the winter.

The coyote's winter diet, while present in this community, is primarily the small rodents that are active at that time of the year, namely, the white-footed

mouse, woodrat, and the cottontail, but they are known to eat almost anything available in the line of animal life, as well as fruits, berries, and vegetation. In the open season the two species of chipmunks, and for a shorter period the mantled ground squirrel, form an important part of their diet. They kill some adult deer in the summer but there is no heavy loss except in the case of fawns from a month to three months old. There seem to be two factors contributing to the heavy killing of fawns, namely: (1) the coyote's ability to locate fawns by scent and (2) their ability to catch them. Very young fawns are not killed as often as older ones are. Experiments with dogs and man fail to show any detectable odor in fawns less than a month or six weeks old.[1] This fact is also seemingly borne out by the method of systematic hunting by sight and sound which a doe uses in locating her fawn after being separated from it. At about six weeks of age the fawns develop the characteristic odor of deer, strong enough to be detected by man upon handling them. Coyotes on three separate occasions were observed trailing fawns by scent, shortly after the average fawn was six weeks old, and numerous kills were located. This predation was highest for a period of about one month, and then decreased. The decrease in numbers killed later in the summer appears to be explained by the ability of the fawn to take care of itself. The coyote appears to eliminate a number of the weaker and more undesirable adult deer during the summer as indicated by the kills examined. This selection should not always be interpreted as betterment, as the inability to escape can be associated with age as well as comparative vigor or undue advantage. An example of undue advantage is given by Hall (1925). He records the killing by a coyote of a Kaibab doe deer while giving birth to a fawn. Groups of coyotes were observed running relays on prime full-grown deer and successfully killing the animal.

The pressure the coyotes exercise on the deer herd is difficult to determine. The Secretary of Agriculture Investigation Committee of 1931 recommended nonhunting of the coyotes, as well as other predators, on the forest. This recommendation is perhaps not as significant in the case of coyotes as other predators, because in point of numbers they have been holding their own and are believed to be increasing over the region.

These observations over a period of three years show the independence of deer and coyote migration and the varying seasonal pressure of coyotes on the deer herd. The number of deer killed per year per coyote can only be approximated. Droppings show deer hair in a higher percentage of cases in deer range, but their habit of eating others' kills and returning to a carcass many times would emphasize the evidence of deer eaten. From this study recent increases in coyote numbers are believed to be due, in part to additional available winter food in form of deer. Also, the number of deer killed per coyote appears to be higher in areas of deer concentration. If true, this could possibly be due to habit as well as availability. There is need, however, of a critical study of the deer-coyote relationship to evaluate these various factors.

[1] Two thousand four hundred and seventy were caught to be hand-reared in the years 1925 to 1931.

Influent mammals of this community are:

Kaibab Squirrel	Tawny White-footed Mouse
Wasatch and Beaver Mountain Chipmunks	Colorado Bushy-tailed Woodrat
Say's Mantled Ground Squirrel	Plateau Bobcat
Yellow-haired Porcupine	Utah Rock Squirrel
	Black Hills Cottontail

The Kaibab squirrel, a climax influent, is the plateau's most interesting animal, inasmuch as this large, tassel-eared squirrel is absolutely unique, being found only in the yellow pine of the Kaibab Plateau. Its range is not entirely limited to the pure pine forest, as scattered trees of yellow pine occur upward to the top of the plateau, and occasional squirrels are encountered wherever these trees exist (Fig. 14).

The squirrel is a resident animal, active throughout the year. The distribution is remarkably uniform over the area of yellow pine. On the basis of counts at various times of day and in all seasons of 1931, an estimate was made of six to eight squirrels per section throughout the pure stand of forest. Three areas, one near Jacob's Lake, one near the western border of the yellow pine, and a smaller area near Bright Angel camp grounds, gave relatively higher

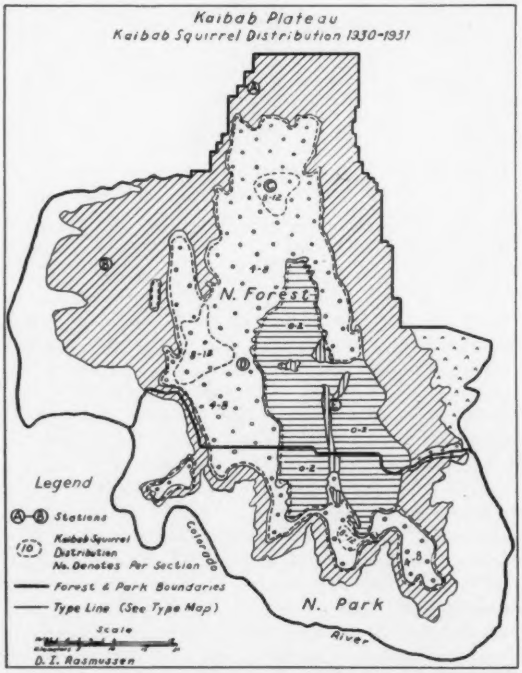

FIG. 14. Distribution and numbers per section (640 acres, 260 ha.) of Kaibab squirrel (*Sciurus kaibabensis* Merriam), Kaibab Plateau, Arizona, 1930-31. Types are same as on type map, Fig. 2.

counts, and it was estimated eight to twelve squirrels were present per section (640 acres, 260 ha.) in these areas. No definite reason (except perhaps additional food in form of camp ground scraps at Jacob's Lake and Bright Angel camp) could be determined for this concentration.

On the basis of mapped vegetation areas there are 387 sections of yellow pine forest and 172 sections of forest above the yellow pine. An average population of seven squirrels per section for pure yellow pine forest and one per section for mixed forest would give a total of 2,900 animals. Interestingly enough, this includes all individuals of a species that are existing in a fairly original situation.

This squirrel has a very restricted diet, feeding almost entirely on the year-old cambium and bark of the terminal shoots of yellow pine (Fig. 15). During

FIG. 15. Main food items of the Kaibab squirrel *(Sciurus kaibabensis)*. Bottom row: remnants of 3 green pine cones left by squirrels after feeding on them. Center row: peeled, year-old twigs from which squirrels had removed the cambium and bark. Top row: discarded terminal tufts of pine needles, current years' growth; all *Pinus brachyptera*.

summer it eats a number of the green pine cones, a small amount of herbage, and occasionally some fungi. Its importance in forest biotics is not very great. At times they do considerable damage to certain selected trees; and in exceptional cases, remains of several hundred twigs may be present on the ground, under a tree, with enough foliage removed to reduce materially the total leaf surface. They have no part or interest in the gathering and storing of food, seeds or otherwise, and so are of no importance in that respect.

No interrelation between shrubs and squirrel numbers could be determined either as food or shelter and under these conditions no effect on squirrel numbers could be shown by the overbrowsing. The number of squirrels in 1931 was at a higher figure than in the preceding four years. There has seemingly been a small increase of numbers for four or five years. The only other information on changes in numbers is the report by the Forest Supervisor in 1919 of a decrease. He says, "Squirrels seem to have suffered considerable loss last winter (1918-19), cause of which is not known" (Kaibab National Forest Reports 1905-39).

Two chipmunks are present throughout this community, and although they are more abundant along the forest edge and in rock habitats, there are numbers of them throughout the open yellow pine forest. They climb readily and forage in trees and bushes as well as on the forest floor. The small Wasatch chipmunk is perhaps the most abundant species; the difference, however, is not great, as the slightly larger Beaver mountain chipmunk is also very abundant. The numbers caught in traps near station C at Jacob's Lake show nearly a fifty-fifty ratio. Within the unbroken forest, however, the Wasatch chipmunk appears as the more abundant species. The attempt at exact estimates of chipmunk numbers is very difficult. The rapidity with which they assemble at available food, such as grain or scraps from camp, is hard to explain on the basis of what appears as an average population of three to five per acre. This estimate is based on trapping and observation in undisturbed localities.

The activity of the chipmunks appears to be a matter of direct response to weather. Some few were abroad in the yellow pine before the snow was entirely gone in early April (1931) and two were seen on a warm hillside at 8,200 feet (2,500 m.) elevation as late as the first week of November. The time when they are most active above ground and the greatest number are in evidence is from the middle of April until early October, but late storms in spring or early fall storms limit this activity. The young ones appear above ground near the middle of June.

The mantled ground squirrel is found throughout the montane forest above the piñon-juniper. Although a ground squirrel of the forested areas, it is not found in deep forest but prefers forest edges and open areas. They are most abundant at the upper edge of the yellow pine, and decrease in numbers to some degree in the higher forests and toward the lower edge of the pine forest.

Their usual abode is a burrow of their own digging or a nest under rocks or fallen trees, although in a number of places they were observed occupying the burrows made by the pocket gopher, which were well out in the mountain meadows.

The season of activity is very short in this species. In 1931 near station D, at Dry Park Ranger Station the mantled ground squirrel was first observed above ground on May 16. They were active and numerous all summer; the numbers were augmented two or three times with the appearance of the young above the ground about the first of August. Their activity continued until a thinning out of numbers was shown in early September, and the last individuals, the season's young, were last seen on September 26. The animals transported a large amount of food to their burrows but differed markedly from chipmunks in that they became extremely fat late in summer.

The food of both chipmunks and ground squirrels appeared to be very similar, consisting of most of the available seeds of herbaceous plants, especially grasses and composites. Their diet also included some green vegetation and anything available in the

line of berries and seeds of trees. Figure 7 shows the evident relative abundance of the species and distribution of the three species.

The porcupine is a widely distributed influent, resident and active year-long in the entire coniferous forest of the plateau, in the spruce-fir, the yellow pine, and the piñon-juniper communities. It shows a preference for yellow pine, and on many areas fifteen to twenty-five percent of the trees have signs of porcupine damage. South and southwestern slopes and trees of less than average vigor seem to be preferred. The damage is serious when the trees are small and the cambium is removed completely from around the trunk, causing the top to die; or when the tree is but a seedling and is completely girdled causing death to the tree.

Porcupines did not feed on conifers to any great extent during summer. From observation of these animals along forest roads, in mountain meadows and parks, and from more than a score of stomach analyses, the summer food shows a preponderance of netted-veined leaf material.

The almost total independence a porcupine shows in its wanderings on the ground away from any tree or retreat and the infrequency of evidence of their being killed by natural predators, appear as proof of the animal's ability to take care of itself. Coyotes ate with relish porcupines that were killed by man and there was evidence that on rare occasions they feasted on a fresh kill of their own. Cougars more than coyotes left evidence of having killed and eaten porcupines.

Numerous porcupine females were killed and examined. All pregnant females had but a single embryo. On the evening of May 9, 1931, five female porcupines were killed near VT Park. Two showed definite signs of having given birth to a single young a short time before. The left horn of the uterus was swollen and inflamed and milk was present in the four most pectoral teats. The other three each contained a single fully-developed young. Two of these young were kept for observation in daylight. The next forenoon they were both active and hungry, and weighed 1⅛ and 1¼ pounds (510 and 565 g.). They were covered with short quills and were quick to assume the defensive attitude upon any sudden movement or noise.

Although the distribution of the porcupines is general this animal occurs in large numbers in certain favorable localities and along their regularly used lines of travel. The old Dry Park Ranger log cabin was visited nightly by porcupines attracted by salt about the doorsteps. A coyote trap caught twenty-three individuals in twenty-five consecutive nights during June and July of 1929. At the same place, in June of 1930, eight more were killed, at which time the cabin was abandoned and no further attempt was made to keep the animals from gnawing on it.

On the National Forest porcupines have been killed by forest officers at the rate of 150 to 200 a year. The numbers have shown no marked change, but indications in 1931 were that they are increasing.

Porcupines have not been killed on the National Park. In 1931 they were extremely abundant, doing considerable damage to the conifers within the park. There is an estimated three to five porcupines per section of forest over the entire plateau.

The most abundant mammal is the omnipresent tawny white-footed mouse. It is present in all parts of the yellow pine community. There is an increase in numbers over the piñon-juniper community, but there are not as many present in the yellow pine association as are found in the higher forest. There is some increase in numbers toward the upper limits of the community.

Mammals of minor influence because of their scarcity are the bushy-tailed woodrat, the bobcat, the rock squirrel, and the cottontail. The woodrat is found in this association and above but its natural distribution is limited by locations of suitable rocky habitats. The bobcat is found in the lower portions of this association, and its range is also limited to ledges and canyon walls. This is also true of the rock squirrel, which is present in local rocky and brushy slopes. It occurs only in the extreme lower edge. The cottontail is present in small numbers throughout the forest, their distribution being dependent upon suitable cover.

Birds

Resident birds of most abundance and importance in this community are:

Pigmy Nuthatch	Cassin's Purple Finch
Long-crested Jay	Red-shafted Flicker
Sharp-shinned Hawk	Red-backed Junco
Rocky Mountain Nuthatch	Western Goshawk
Mountain Chickadee	Western Red-tailed Hawk

A monotonous pine forest with a single conifer as the dominant is not conducive to a large bird population. The species that occur are quite uniform throughout the forest. The forage niches of the birds present are distinctive. In most species there is a wide range in food but a limited range in territory or strata covered, such as tree trunks, ground, limbs, twigs, and crowns.

Of the resident birds the pigmy nuthatch is one of the most uniformly distributed species, and it is limited to the yellow pine forest. It forages about small limbs and twigs.

The long-crested jay is a year-long resident of the forest above the piñon-juniper. Although occasionally seen on the ground, its usual activities are in the yellow pine trees.

The sharp-shinned hawk is an influential resident, although it is not abundant. Nuthatches and the Audubon warblers seem to suffer most from this predatory species, but no species are exempt from its attacks.

The Rocky Mountain nuthatch is abundant in the yellow pine, although its range extends above this community to some extent. It is not as abundant as is the pigmy nuthatch.

The mountain chickadee breeds throughout the montane forest and is found in the yellow pine, but is much more abundant in the higher forest. This is also true of the Cassin's purple finch.

The flicker's abundance is influenced by the presence of aspens, although not limited to it, inasmuch as the bird usually nests in aspen. This bird shows a great amount of vertical migration.

The red-backed junco is resident in this association and in the forest above. It is most abundant near the upper part of the community and in many areas is the most abundant bird. Its distribution, however, is not uniform.

The goshawk is a bird of considerable importance in the interactions of this community. Only its scarcity prevents its from being a major influent. Although Arizona is considered to be the extreme southern tip of their breeding range, birds were seen during all months over three summers of study. It was estimated in 1931 that there was one goshawk per 5 sections. In the same year a nest was located and observed from the time the eggs hatched until two young birds left it. Observations of food habits showed that adult hawks feed mostly on birds, but caught rabbits, the mantled ground squirrel, the Fremont chickaree, and the Kaibab squirrel. No great inroads were made on the Kaibab squirrel, although these hawks are known to have eaten them.

Because of interest in the food of the goshawk a number of pellets were collected from under the nest of the bird during the first week of July 1931. Dr. Clarence Cottam of the United States Biological Survey gave the following identification of the material contained in them:

"Name: *Astur atricapilus*, Number: B 2956, Type: Pellet debris.

Food contents: Fragments of rabbit, fragments of 1 Sciuridae, fragments of *Colaptes c. collaris*, fragments of 1 *Cyanocitta s. diademata*, fragments of 1 ? *Dendroica* sp., undetermined feather fragments, part of which appeared to be from a woodpecker, possible *Sphyrapicus* sp.

Secondary or accidental food or food of undetermined origin: Fragments of: 1 Orthoptera, 3 *Camponotus* sp., 58 *Formica* sp., 6 *Myrmica* sp., 12 *Lasius* sp., 16 *Pogonomyrmex* sp., undetermined Hymenoptera, 1 Carabidae, 1 Chrysomelidae, 1 Buprestidae, 1 Tenebrionidae, 3 Lepidopterous larvae, 20 or more *Symphoromyia* sp., Dipterous pupae cases, needles of ? *Abies* sp., *Picea pungens*, *Pinus* sp., undetermined plant fiber."

The western red-tailed hawk is present throughout the montane forest during the summer, but is much more abundant above the yellow pine. It forages regularly in the meadows and parks, in contrast to the goshawk, which is encountered as it flies low and swiftly under the trees. The red-tailed hawk feeds primarily on rodents, and the main article in this community is the mantled ground squirrel and the chipmunks. Cases where this hawk has killed Kaibab squirrels are known.

The common or characteristic open season birds are:

Chestnut-backed Bluebird	Western Chipping Sparrow
Audubon's Warbler	Horned Owl
Natalie's Sapsucker	Band-tailed Pigeon

Of the open season birds the chestnut-backed bluebird is the most characteristic, as well as an abundant bird of the yellow pine. Although migratory, it was present in early April, and numbers were observed within the yellow pine as late as October in 1931.

The Audubon's warbler is perhaps the most abundant bird in the pure yellow pine forest, but is also present over the entire plateau. They forage about the crowns and terminal branches of the trees, where one usually locates them by their short flights out and back from the periphery of the tree. This is in decided contrast with the usual warbler activity.

The sapsucker is a very common bird. It usually nests in the aspen, but feeds a great deal on the cambium layer of the smaller yellow pines.

The chipping sparrow is common in this association, as it is over the entire plateau, but it is in this community that it is most abundant. Its favorite location is the open spaces and groves of the young pines that are typical here.

The horned owl is present in this community, but due to its retiring habits is seldom seen. They are often heard, and they forage out over the meadows and through the forest. The common nocturnal species of mammals, as Thomomys and Peromyscus and Microtus, are their main source of food.

The band-tailed pigeon, although uncommon, occurs here as a summer resident. It is very spotted in distribution. Formerly it was much more abundant, and reliable sources report great flocks that visited the plateau and fed on the berries. Certain of these berries, such as serviceberry (Amelanchier) still exist in some numbers. All of the species of berries of which the forage is palatable to deer have been reduced, and some have been killed completely.

The winter resident birds include a small increase in population of juncos. Other than that there is very little change involving an increase of species. The forest of pure yellow pine with all the herbaceous species covered by snow offers little in winter for residents and less for immigrants.

Reptiles

The single reptile that is represented in any numbers in the yellow pine community is the horned toad. It occurred throughout the association, and was most abundant where the trees were so spaced that a great amount of sunlight reached the ground.

Invertebrtaes

Regular quantitative invertebrate collections were made at the two stations, C and D, in the yellow pine forest. Collections were taken from the ground and herb strata, and sweepings from the yellow pine were made at shrub height (three to five feet, .9 to 1.5 m.) and at a low tree height (fifteen to twenty feet, 4.6 to 6.1 m. above ground).

In point of numbers the very small species of jumping plant lice, Chermidae, plant lice, Aphidae, and

leaf-hoppers, Cicadellidae, were most abundant on the yellow pine, in both the small trees and crowns of the larger trees. Of the chermids, *Psyllia americana* Crawford, *Paratrioza cockerelli* (Sulc.), and *Trioza arizonae* Aulmann were collected, the latter species being the most abundant of the three. The aphids present belonged to the genera Eulachnus and Cinara. One species of leaf-hopper or Cicadellidae was very abundant; two others were common. The abundant spiders were the immature of *Aranea cucurbitina* Clerck, *Linyphia (phrygiana?)*, *Dictyna* sp., and *Dendryphantes* sp. A large weevil, *Tricolopis inornata* Horn, appeared in a great number of the collections, and flies of family Anthomyiidae, and gall flies of family Cecidomyiidae were abundant.

Ecologically the ants are perhaps the most important invertebrate group of the arid forests. They are abundant in the numbers of species and of individuals. Eighteen percent of all invertebrates taken were ants. In their activity a number of the ground species are found high in the trees and are common on the lower trees. These include *Lasius niger* var. near *sitkaensis, Formica fusca* var. *subaenescens* and *Formica* (Proformica) *neogagates lasioides* var. *vetula*. A sawfly of genus Xyela, a Geometrid larva, and the western syrphid fly, *Syrphus opinator* Astan Sacken, whose young feed on aphids, were also definite components of these strata.

The herb and grass stratum does not have a distinctive population here as is often the case. The vegetation covers only two to ten percent of the ground surface. This gives a mixture of herb and ground species of invertebrates, and the occurrence of species that are usually found in such type of habitat. The most conspicuous elements are the banded-winged locusts or Oedipodinae. These normally rest on the bare ground and feed on the herbaceous species. Numerous immature and a number of adults were collected in quantitative collections. The most abundant species, in order of their numbers, were: the yellow-winged locust *Trimerotropis suffusa, Trimerotropis pallidipennis pallidipennis,* and *Circotettix coconino,* all species showing preference for the fairly open and more sunny areas within the yellow pine forest.

The two aphids, *Aphis* sp. and *Macrosciphum* sp. (not *packi*), were abundant on herbs, as were the leaf-hoppers, *Cicadellidae* spp. The spiders, *Philodromus pernix,* and *Linyphia phrygiana?* and the chermid, *Paratrioza cockerelli* (Sulc.) were also common species.

On the ground the abundant species were the same ants that are named in tree strata species and also *Myrmica scabrinodis* var. and *Liometopum apiculatum luctuosum*. A carabid beetle, *Dyschirius globulosus* Say, a tenebrionid of genus *Eleodes* and the centipede, *Scolopendra polymorpha* Wood were present. Following the summer rains the soil contained myriads of Collembola, which were not in evidence earlier in the season.

A very common and definite type of microhabitat existed throughout this community in the form of dead yellow pine trees. Dead trees occur naturally throughout the forest, and some in all stages of decomposition are found. The presence of any healthy trees that are being killed at the present time by insect infestation is extremely rare or lacking, but there is normally a loss of some trees by old age, lightning, mistletoe, and other causes.

The plateau shows evidence of numerous former insect infestations. There are large areas, bug kills, covered with dead trees; some of these are extremely old, others of very recent date. The insect responsible, no doubt, for most of them is the Black Hills beetle, *Dendroctonus ponderosae* Hopkins. Collecting and cruising failed to show the presence of a single live specimen of this beetle during the three summers of 1929, 1930, 1931, yet the beetle was epidemic on the plateau from 1920 to 1925 and killed an estimated 15 million feet of standing yellow pine.

In trees that are freshly killed or weakened by the former attack of *D. ponderosae* Hopk. there were great numbers of engraver beetles, *Ips integer* Eichh. In trees that had been dead several years there were the beetles *Hylurgops subcostulatus* Mannh. and *Rhyncolus* sp., and penetrating the woods were the shot-borers, *Orthotomicus ornatus* Sw. Under the bark of all dead trees of all ages was the large black ant, *Camponotus herculeanus* var. *modoc.* (Whlr.), and the smaller one *Camponotus maculatus vicinus* var. *niti divertris* was also frequently found. Late in the summer the large winged form of Camponotus was extremely abundant throughout the forest.

The absence of Mollusca is striking; none were found on the vegetation or ground surface. One species, *Oreohelix strigosa depressa* (Cockerell), occurs several feet below the ground surface, among rocks and ledges, and is rarely seen near the surface, and then only following rains.

In point of number of invertebrate animals present, the two stations showed a surprising agreement of numbers and seasonal abundance for the ground surface, herbs, and tree strata. The station collections averaged near .22 million per acre (.55 ha.), with a single serotinal maximum of about .36 million per acre (.90 million per ha.). (See Fig. 12.)

There was not the distinct bimodal curve of the piñon-juniper community; the vernal increase was later; the autumnal decrease began earlier. The population curve showed an early increase in the number of insects of the yellow pine (sweepings made of the terminal branches), followed by a fairly gradual decline in the numbers obtained in the collections. In the herbs the maximum number collected at both stations was in the twenty-sixth and twenty-seventh weeks (early July), and in both cases there was a considerable number at this stratum until the thirty-sixth week (September 1). The number on ground stratum varied, but no significant changes were apparent during the season.

In each station the smaller yellow pine trees (those less than six feet tall) were swept. This was done to determine the difference in invertebrate population of pines, those very severely browsed as compared

with those browsed only slightly. At station D the small trees had the appearance of artificially trimmed conifers, with the periphery of the tree a compact growth of needles, due to the deer's constant check on them.

At station C trees were of nearly normal reproduction. The numbers of invertebrate animals present under these two conditions differed greatly. There were nearly twice as many in the sweeping from the browsed pine. The species were, in the main, Aphidae, Cicadellidae, Chermidae, and ants. There was an increase of certain smaller invertebrates with the compact arrangement of the needles; also, the yearly browsing left the trees somewhat damaged and the wounds caused by such attacks attracted certain species. The damage resulting from the increased infestation is perhaps of minor importance in comparison with the effect on the trees of losing their terminal shoots each spring, year after year.

Within the yellow pine association of the montane forest biome, the invertebrate population showed some definite characteristics, namely:

(1) Greatest summer population in the herb stratum.

(2) Early seasonal maximum in invertebrate population of yellow pine.

(3) No significant variation shown in ground species.

(4) A marked increase of invertebrates on heavily browsed trees.

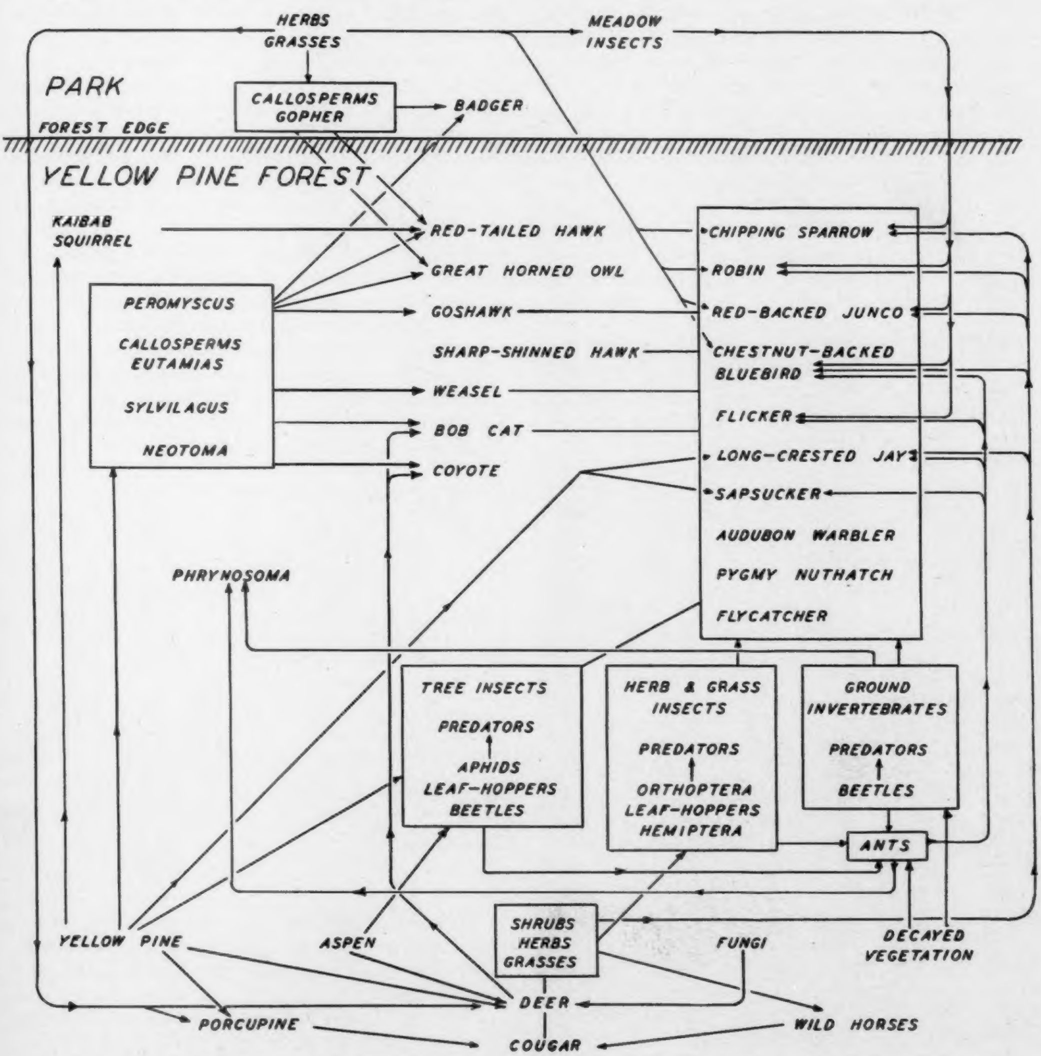

FIG. 16. Diagram of food chain or food coaction within climax yellow pine forest and bordering grassland. Arrows point from animals or plants eaten to the animals that eat them.

(5) The presence of great numbers of insects not obtained by sweeping, as shown by foraging habits of certain birds.

(6) A very definite microhabitat in the form of the dead yellow pine trees, the invertebrates of which are of considerable importance in the community, but are independent of usual stratification.

Figure 16 pictures diagrammatically the food chain or food coaction with the yellow pine community and bordering park of grassland.

VIII. THE MONTANE FOREST CLIMAX

THE *Picea-Abies-Sciurus fremonti* ASSOCIATION

GENERAL

A mixed coniferous forest occurs above the yellow pine. The uniformity of its physiognomy and similarities as concerns many influent animal species lead to its consideration as a single large biotic community, although the dominant trees that are present there have been given as typical of the two plant formations, i.e., montane and subalpine (Clements, '16).

This mixed forest occurs above an average of 8,200 feet (2,500 m.) elevation and includes the highest portions of the plateau. It has an area of 112,200 acres (45,400 ha.). A number of the dominant trees occur at lower elevation on cool slopes and in the canyons some below 6,800 feet (2,075 m.) within the Grand Canyon.

FIG. 17. Montane forest climax (*Picea-Abies-Sciurus fremonti* Association).

The forest differs greatly in appearance from that of the yellow pine (Fig. 17). The trees are closely spaced, and in certain localities there is a great amount of fallen timber, making travel through the forest extremely difficult.

VEGETATION

The dominant trees are the two spruces, *Picea engelmanni,* and *Picea pungens;* the Douglas fir, *Pseudotsuga taxifolia;* the white fir, *Abies concolor.* Aspen, *Populus aurea,* and yellow pine, *Pinus brachyptera,* occur throughout the forest, but appear to be of secondary importance.

The occurrence of the trees is uniform only in a general way. *Abies concolor* and *Pseudotsuga taxifolia* extend downward slightly more than do the spruces, but they also dominate the highest ridges. *Picea pungens* shows a preference for the edge of meadows; the *Pinus brachyptera,* when it occurs in any numbers, is on the more exposed hillsides. *Populus aurea,* although a subclimax tree, is present throughout the forest; very few, if any, forest areas of an acre or larger show an absence of this species. Other areas show definitely the reproduction of spruce under the aspen. In some local areas the aspen forms practically pure stands.

Throughout the community, but especially abundant at the higher elevations, is the dwarf juniper, *Juniperus communis.* At some localities it forms a definite shrub stratum. This is the only shrub of great importance and is the single species other than tree species that appears to be of major importance. A few individuals of alpine fir, *Abies lasiocarpa,* are present near the summit of the plateau, but occurrence is too rare to be important.

Sample counts of tree species present in this association are shown in Table 6.

TABLE 6. 1/10 acre (1/25 ha) of mature spruce-fir forest. 9,000-foot elevation. VT Park, Arizona.

	Seedling	1–6	6–12	12–18	18–24	24–26
North-facing slope 10% grade						
Diameter breast high in inches						
Picea engelmanni	23	20	10	10	6	1
Pseudotsuga taxifolia	23	23	4			
Abies concolor	1	3	1	1		
Populus tremuloides aurea	1	3	2	1		
Juniperus communis	2*					
South-facing slope 10% grade						
Picea pungens					14	
Populus tremuloides aurea	7					
Juniperus communis	38*					

*Mature shrubs.

There are a number of shrubs of minor importance. *Symphoricarpos* sp. is found in the more open situations. This shrub has, in the past, been a conspicuous plant, but has been greatly limited by the deer. It now occurs as small, compact bushes showing the result of heavy summer overbrowsing or as dead bushes. Numerous dead plants of this species are present. There are a number of old dead willow,

Salix sp., showing evidence of having been killed by deer browsing. It is doubtful that more than a few individuals of this species are now alive on the summit of the plateau, and a few years of current usage will completely destroy the evidence of its former occurrence. *Odostemon repens* is present in considerable numbers, and there are a few individuals of *Ceanothus fendleri,* and a species of Chrysothamnus in certain localities.

Ordinarily a forest of this type contains a great number of seedling aspens, but the numbers that are present on the plateau from 1929 to 1931 could almost be enumerated. From examinations of young aspen trees and shoots there have been extremely few young trees established during the period of 1916 to 1932. Only the exceptional tree has been able to grow tall enough to get out of reach of the deer during that period.

Where the conifers and aspen occur in compact stands, there is very little growth of herb and grass species. A few characteristic plants occur, but the area is extremely poor in the amount of this type of vegetation.

Beneath the heavy forest there exists a great amount of lichens, liverworts, and mosses. A species of Carex is the most abundant seed plant. Two shinleaves, *Pyrola secunda* and *P. picta,* are both typical of this situation. The common plants occurring where there is not complete shade are the *Fragaria platypetala, Antennaria* sp., the *Geranium fremontii,* the grass, *Bromus porteri,* and the twinflower, *Linnaea borealis americana.* Where there is considerable penetration of sunlight one finds many of the meadow herbs, or *Potentilla* spp., *Silene douglasii,* and *Erigeron* spp.

The combined rainfall for July and August averages in excess of five inches and under usual conditions there is production of enormous quantities and a great number of species of fungi throughout the whole montane forest, but especially in these higher areas. Here they grow abundantly over the forest floor and the meadows, often several per square meter, and many species growing to large size. During 1930 over twenty varieties were distinguished on the plateau. They were very palatable to the deer and they apparently fed on all of them, including certain of the poison amanitas. The red amanita, *Amanita muscaria,* was the most abundant; it grew to large size and was readily eaten by both deer and the chickaree. There was, however, no evidence of sickness or death resulting from their eating any of this species. The most conspicuous fungi were several species each of Boletus, Boletinus, Russula and Amanita. In addition there were species of Agaricus, Coprinus, Collybia, Clitocybe, Cortinarius, Marasmius and others. Also large numbers of the puff balls, Lycoperdon and bracket fungi, Polyporus.

MAMMALS

The mule deer is also the most important animal here in point of influence on this biotic community. If an animal becomes dominant on land, it would be of the type demonstrated here, where it exercises an influence over the entire community, changes the natural order of things, prevents the growth of several species of woody plants, and by selective browsing favors other species.

The deer enter this community in early May, and remain here until storms drive them out in late September or October. The number per unit area here is not as significant as in the two other forest communities. The distribution is greatly influenced by the presence of meadows, thin stands of trees, open hillsides, and a variety of local conditions. The existence of a compact growth of timber provides extremely poor deer range.

There is a concentration of deer about VT Park, as shown by the map of deer abundance (Fig. 11). This area of forest in vicinity of VT Park is nearly devoid of deer food; the proximity of the meadows explains their presence, although they normally spend their days in the forest. They come a distance of one mile (1.6 km.) from back in the forest to the open meadows during early summer. On the basis of deer seen in the meadow and deer remaining out of the meadow, but in nearby areas, there are estimated 45 deer per section (640 acres, 260 ha.). This is the area of greatest summer concentration.

With the appearance of great numbers of fungi in the late summer of normally wet years, the majority of deer forsake the meadow and the distribution is fairly uniform through the forest.

It is impossible to say what percentage of the various plants were utilized by the deer as food under former conditions. At the present time, there is an unnatural condition as shown by the complete elimination of some species. Field observations, in addition to stomach analyses of twenty deer killed by cars and predators, have provided data for summer section of deer's food habits diagram (Fig. 18).

The following general statements can be made concerning the deer in this community:

1. The more desirable food plants have been eliminated or greatly limited in the amount of available forage.

2. Of the dominant tree species deer eat a great amount of *Abies concolor, Populus aurea,* and *Pinus brachyptera.* They eat a small amount of *Picea pungens* and *P. engelmanni* and *Pseudotsuga taxifolia,* and rarely *Juniperus communis* and *A. lasiocarpa.*

3. Netted veined plants make up the greater bulk of their food. There is a wide variety, but considerable selection of desirable species.

4. There is a very definite seasonal selection; for example, yellow pine is eaten mostly in early spring, as are certain pre-vernal and vernal herbs; aspen shoots are eaten in greater amounts in late summer, and certain species of the genus Lupinus are heavily utilized in the late summer and fall, but show little usage during summer.

5. Use is made of food that is available for short periods, as aspen leaves, which may make up seventy-

five percent or more of the stomach content of deer killed in early fall. Mushrooms often compose fifty percent or more of deer food for a period in late summer.

6. Extremely little grass is eaten, even with the paucity of preferred foods. Grass rarely consists of as much as fifteen to twenty percent of the food eaten and more often is less than ten percent.

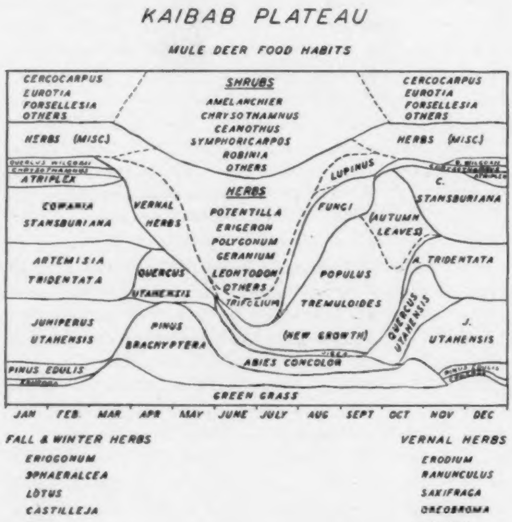

FIG. 18. Generalized year-long food habits of mule deer, Kaibab Plateau, Arizona, 1929-1931, inclusive. Height of graph equals total food taken by deer spending summer at higher portions of the plateau and migrating at peaks of migration. Based on analysis of approximately sixty stomachs and year-long field observations.

The coyote occurs here in numbers of thirty-six to forty per township during the open season; a few remain here all winter. Their main summer food is the small rodents Peromyscus, Citellus, and Eutamias, supplemented by a variety of minor foods, including a large number of Orthoptera. There is no marked difference in the relation of the coyote here and in the yellow pine community to rodents and deer.

Influent mammals of lesser importance are:

Fremont Chickaree	Beaver Mountain Chipmunk
Yellow-haired Porcupine	Wasatch Chipmunk
Tawny White-footed Mouse	Colorado Bush-tailed Woodrat
Mantled Ground Squirrel	
Arizona Weasel	

All of these animals, excepting the chickaree or the red squirrel and the weasel, have been discussed in their relation to the biotics within the yellow pine community of the montane forest. The difference is not great as concerns their activity and importance in the spruce-fir. There is some change in relative abundance and in the difference in population per unit area. Some differences between the yellow pine and mixed coniferous forests are shown in their abundance (Fig. 7).

The chickaree is a climax influent and occurs throughout this community. Its distribution is confined to areas where Abies, Pseudotsuga, or Picea occur. This is true at the extreme lower borders of the association, where the lowest extension of any one of these trees marks the lower limits of the squirrel's range. But at these lower elevations the squirrel middens show great preponderance of yellow pine cones. This squirrel, because of some factor other than food, perhaps shelter, does not occur in the pure yellow pine forest.

During late August, while gathering the cones of *Picea pungens,* they appeared in numbers of several per acre in the narrow strip of the blue spruce along certain meadows. On the basis of early summer counts, it was estimated that there was one squirrel per fifteen acres (six ha.) of mixed coniferous forest.

The food of this squirrel is a variety of seeds of conifers and some few herbs and fungi. It is active the year-long, but depends upon its caches of food for winter subsistence. These food stores showed a preference for *Picea pungens* and *Pseudotsuga taxifolia,* with some *Pinus brachyptera* and *Abies concolor.* The latter two were eaten in large quantities during late summer. Their habit of storing mushrooms is usually shown by investigations of their caches in the fall. Mushrooms drying on the limbs of conifers are a familiar sight during the late summer.

There is a little overlapping of range of the chickaree with Kaibab squirrel, but no great mingling or avoiding of each other. The distribution of both species can be explained purely on the basis of the presence of certain conifers.

The weasel occurs throughout the montane forest. It is more in evidence in the higher forest, due, no doubt, to relative greater abundance of rodents. Individuals were observed killing Citellus and Eutamias.

The porcupine is more numerous per unit area than in the yellow pine association.

The chipmunks are more abundant in the spruce-fir than the yellow pine, but the great amount of suitable habitat of forest edge type seemed to be the factor accounting for this. The ratio of species was changed. Instead of a one-to-one ratio that exists within the yellow pine, here there are four or five *Eutamias adsitus* to each *E. minimus consobrinus.*

The tawny white-footed mouse is common, but not as abundant as in the yellow pine association.

BIRDS

Although the mammal species were fairly well distributed over both the yellow pine and mixed coniferous portions of the montane forest, many bird species show marked selection for one or the other of these associations. Certain species are wide-ranging; others, especially the open season birds, are typical of the spruce-fir community.

A number of species are closely associated with the aspen, and its occurrence throughout this community

accounts for distribution of part of the species, while the mountain meadow-montane forest border accounts for a number of others.

Resident birds of the community are:

Long-crested Jay	Sharp-shinned Hawk
Mountain Chickadee	Red-backed Junco
Alpine Three-toed Woodpecker	White-breasted Woodpecker
	Rocky Mountain Nuthatch
Dusky Grouse	Red-shafted Flicker

Open season birds are:

Mountain Bluebird	Cassin's Purple Finch
Pine Siskin	Western Robin
Natalie's Sapsucker	Western Evening Grosbeak
Olive-sided Flycatcher	Wright's Flycatcher
Violet-green Swallow	Western Ruby-crowned Kinglet
Audubon's Warbler	
Western Warbling Vireo	Western Chipping Sparrow
Audubon's Hermit Thrush	Townsend's Solitaire

The greatest bird population of the plateau occurs along the borders of the meadow. The robin, mountain bluebird, flycatchers, chipping sparrow, junco, and flicker are typical here. The warbling vireo shows a preference for a forest of aspen. The deep forest has the Audubon's hermit thrush and the Townsend's solitaire. In the tree-tops the purple finch and evening grosbeak are found. The terminal limbs are forage ground for the kinglet and the chickadee; the limbs and tree trunks for the woodpeckers, nuthatch, and sapsucker, and oddly enough, the long-crested jay. The dusky grouse occurs in certain local areas near the canyon rim, usually in localities that have abundant growth of *Juniperus communis*. A number of the species present only in the open season in this community were present in winter around the base of the plateau and are in reality year-long residents of the plateau.

Area counts differ greatly for bird populations. A forest edge of blue spruce and aspen gave in a selected two-acre (.81 ha.) plot the actual nesting records in 1931 of nine pairs of birds: two kinglets, two chipping sparrows, one chickadee, one olive-sided flycatcher, one warbling vireo, one mountain bluebird, and one flicker. This area included the VT Ranger Station, at an 8,900-foot (2,715 m.) elevation.

IX. MOUNTAIN GRASSLAND

Stipa-Carex-Thomomys ASSOCIES

MEADOWS AND PARKS

There are some 10,000 to 15,000 acres (4,000 to 6,000 ha.) of open parks and meadows present on the entire plateau. These vary greatly in size, but are very similar in their general appearance and features. They are located, as a rule, in fairly level basins and in the bottom of shallow valleys.

Certain localities show an interesting phenomenon in the presence of a near timber-line or Krumholz condition along the meadow border at the foot of a forested slope at an elevation of 9,000 feet (2,740 m.). A factor study in VT (De Motte) Park, the Plateau's most famous park, showed a marked difference in daily minimum temperatures in adjacent forest and meadow (Fig. 4). (Mead, '30.)

Care, however, must be used in not assigning the environment created by the forest as the explanation of its presence. Climatic factors, influenced by air currents and soil differences, may account for the occurrence of these parks and meadows. Explanation of these areas as resulting from forest fires does not seem reasonable on the Kaibab Plateau. There is a usual growth of small conifers along their edges, giving the appearance of invasion of forest species. These trees, however, show by the annual growth rings that they are much older than they appear. Sample blue spruces of less than five feet (1.5 m.) in height present on the edge of the meadow showed as many as thirty annual rings. But in the forest proper, fifteen to twenty feet (4.6 to 6.1 m.) from the edge of the meadow, spruces of six inches (15 cm.) diameter and thirty-five feet (11 m.) height were shown to be the same age.

VT Park, the second largest park of the plateau, and named from the cattle brand of the first large cattle outfit that controlled the area, has an elevation of 8,800 to 9,100 feet (2,680 to 2,775 m.) and an area of approximately 3,000 acres (1,200 ha.). The main road to the north rim extends the length of the park, and this is the location in which deer are most abundant during the summer and most often seen by visitors to the Kaibab.

The explanation of deer presence and variation in numbers in the meadows has been one of the interesting features to observe during this study. Figure 19 shows the evening counts in the northern end of VT Park during the summers of 1930 and 1931. This is an area of 750 acres (305 ha.) bordered by spruce-fir-aspen forest. The maximum number of deer visiting the area is believed to represent near the total population for a radius of one mile (1.6 km.) of the meadows or 2,500 acres (1,000 ha.) of forest.

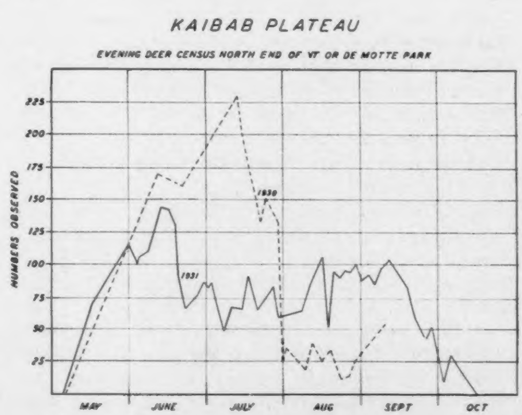

FIG. 19. Evening deer census at the north end of VT (De Motte) Park, Kaibab Plateau, Arizona. Counts made at sundown during years 1930 and 1931 in an area of approximately 750 acres (305 ha.).

The 1930 and 1931 data differ markedly in two respects, namely, (1) maximum number of deer in 1930 is greater than 1931. This appears to be indicative of differences in total summer population between the two years, although perhaps this is somewhat exaggerated; (2) the marked difference in late summer population between the two years is directly correlated with precipitation. In 1930 the first heavy summer rain storm occurred on July 12, and storms continued regularly during the remainder of July and August, resulting in the production of enormous numbers of mushrooms. The deer left the meadow and were observed throughout the montane forest feeding on the fungi. A similar change in numbers occurred in 1929, also a year with abundant late summer rains. In 1931 the first heavy summer storm occurred on July 28-29, but rains did not continue after that time. No mushroom crop was produced that year. Deer continued to visit the meadows until the aspen leaves began to fall, although under these dry conditions the mountain clover in the parks provide very little of the late summer food.

FIG. 20. Fenced plot at border of mountain park summit of plateau, showing growth of quaking aspen, *Populus aurea* and spruce, *Picea pungens*, when given eight years protection from deer browsing. Spruces are hedged and no aspen are conspicuous enough to show on picture outside of plot.

The sex ratio of the deer herd differed in different localities during the summer, but was consistent on individual areas. The group in the north end of VT Park, exclusive of fawns present in late summer, averaged 60% does, 23% yearlings, and 17% bucks during 1931. During the same year a herd in the southern part of VT Park consisted of 61% adult bucks, 11% yearlings, and 28% does. A small number of fawns appeared in the meadow during late August and September. Maximum counts of the southern herd were 288, June 22, 1930, and 188, August 10, 1931.

From all evidence, it appears that the habit of the deer of visiting the meadows as they now do is a fairly recent change in their activity. The livestock men who have spent years on the plateau say that deer first began visiting the park in large numbers about 1916 and that before that time there was little or no use of the meadow by the deer. T. G. Pearson (1925) reported counting 1,028 deer on the evening of August 21, 1924. This was at the time of maximum numbers visiting the meadow. The present poor condition of adjoining summer range and small amount of available food indicated that the deer, by all evidence, were forced into the meadow in order to obtain forage.

The future existence of the herd will depend on a variety of factors affecting biotic balance. Present indications are that the numbers that visit the meadows will continue to decrease with an increase in desirable forage near-by, and that restoration of near natural conditions to the plateau will limit the number of deer that visit the open parks each evening. This was the situation at the time the area was first set apart as a game preserve. Restoration of the former large show herds would no doubt indicate once again the absence of suitable and sufficient forage in the surrounding forests.

VEGETATION

There are two definite divisions of the meadows that are recognizable. One is the low, more mesic portion, where the deer ordinarily concentrate, and where near 90% of the vegetation consists of netted-veined plants. The bulk of this consists of several species of Trifolium, with dandelions, both Agoseris and Leontodon, a small Erigeron, *Achillea lanulosa*, Potentilla, *Ranunculus subsagittatus*, and *R. alismellus*. Species of Polygonum occur on newer denuded areas. The grass and grass-like species composing about 10% of the vegetation of this part of the mountain meadows are mainly *Phleum alpinum* and species of Poa, Deschampsia and Carex.

In the higher and more xeric portions of the park, the grass makes up near 50% of the total ground cover. The grasses consist of species of Deschampsia and Festuca with *Blepharoneuron tricholepis*, *Stipa comata* and some others. The most conspicuous herb species include species of Antennaria, Eriogonum, Potentilla, Saxifraga, a tall Erigeron, *Phlox caespitosa*, *Pseudocymopterus montanus*, *Actinea richardsonii*, *Orthocarpus purpureo-albus*, and *O. luteus*.

The favorite food of the deer visiting the meadow is several species of the Mountain clover or *Trifolium* spp. This is preferred to all other meadow species. They eat many other herbs readily, but only a very small amount of grass. The two main areas of clover are in close proximity of the only two springs in the park, one north of the VT hotel and one near Mason Well, four miles (6.4 km.) south of the hotel. In the days of big cattle outfits, VT Park was the summer headquarters, and the area was grazed continually by horses and subject to overgrazing by herds of cattle that were collected there.

Influent animals of the meadows and parks are:

Mexican Badger	Colorado Pocket Gopher
Rocky Mountain Meadow Mouse	Mantled Ground Squirrel
Wasatch Chipmunk	Beaver Mountain Chipmunk
Sparrow Hawk	American Raven
Mexican Locust	Pellucid Locust
Yellow-winged Locust	Mormon Cricket

The badger is found at all elevations on the Kaibab where there is grassland or open type of country and a sufficient abundance of burrowing rodents. Its numbers are not great, but one is occasionally seen in the mountain parks and in the sage valleys of the lower portions of the piñon-juniper. Evidence of their digging for pocket gophers and other rodents is often seen. The total estimate for the plateau is 100 to 150.

The pocket gopher is fairly abundant throughout the meadows where the soil is sufficient for burrows and not subject to flooding. It is the only mammal that is regular in its distribution over the meadow. It is active year-long, as evidenced by the earth plugs present over the surface of the ground following the melting of snows. They obtain most of their food by digging, but occasionally one is observed snatching food from near the mouth of its burrow.

The Rocky Mountain meadow mouse is found in the more mesic situations, where there is sufficient cover in the way of rank growing grass. The distribution, however, is limited.

The mantled ground squirrel and the chipmunks have been discussed in relation to forest edges. The ground squirrel, especially, is abundant at the edge of meadows, enough so as to exercise considerable pressure on plant growth.

There are no birds limited to these areas, but the bluebird, the robin, and in late summer, the sparrow hawk, forage regularly over the meadows. All three species were observed feeding on the abundant grasshoppers. During the summer flocks of ravens fed regularly on grasshoppers and the large crickets in these high meadows.

Orthoptera make up the most important invertebrate group in this community. The abundant species are the Mexican locust, the pellucid locust, the yellow-winged locust, and the large western or Mormon cricket.

X. ADJACENT COMMUNITIES

SHORT-GRASS GRASSLAND

Although present vegetation maps fail to show it, there exists at the eastern edge of the Kaibab Plateau an area of some two hundred square miles of grassland. This is Houserock Valley. The severe overgrazing by domestic stock has left only a part of the former ground-cover of sod. The truly good grassland that remains is too far from water for cattle to pasture it closely during the dry season. In years of abundant rainfall the whole area regains, in part, the aspect ascribed to it before the great herds of cattle both wintered and summered there.

The vegetation is dominated by grama grasses, *Bouteloua gracilis* and *B. curtipendula* which in much of the area constitutes a pure sod. Other prominent grasses are galleta grass, *Hilaria jamesii,* and on sand areas, *Sporobolus cryptandrus.* Small areas of false buffalo grass, *Munroa squarrosa,* burro grass, *Scleropogon brevifolius,* crowfoot and black grama, *Bouteloua rothrockii* and *B. eriopoda* are present. There are several species of cacti, *Atriplex canescens,* and a variety of shrub species.

Formerly this valley had abundant pronghorn antelope. One very old Kaibabit Indian, "Indian Charley," tells of trips he made there as a young man to hunt these animals. He reports that the Indians dug pits in which they concealed themselves until the antelope approached near enough to be shot with bows and arrows.

At present this area supports a semi-tame herd of bison that were introduced there several years ago and are now owned by the State of Arizona. Although there are no records of their former existence in this region, the herd of some 200 individuals is very much at home there. It ranges over the area, as the species formerly, no doubt, did in the short-grass plains of western Texas and New Mexico.

The area contains smaller vertebrates typical of the short-grass plains. Two species of kangaroo rats, one known as the Houserock Valley kangaroo rat, pocket mice, the Houserock Valley pocket gopher, grasshopper mice, the horned lark, and lizards of the genera Uta and Sceloporus are common.

There is also an area of short-grass grassland between Kanab Creek and the piñon-juniper and yellow pine areas of Mt. Trumbull. Dutton ('82, p. 104) tells of luxuriant grass present in the neighborhood of Pipe Springs in 1872. He returned ten years later and said, "Today hardly a blade of grass is to be found within ten miles of the spring unless on the crags and mesas of the Vermillion cliffs behind it." Overgrazing by the concentration of livestock about this famous watering hole had changed the vegetation of the whole area in a single decade.

BASIN SAGEBRUSH

Toward the northern and northwestern portions of the plateau there exist areas of *Artemisia tridentata,* an extension of the very generally distributed climax of the Great Basin. The growth is not as rank as in fertile Utah valleys, but the appearance is typical. Like most lowland sagebrush areas in the Great Basin, the associated grass species have almost all been destroyed by indiscriminate and unregulated grazing.

Such characteristic vertebrates as the sage thrasher, the vesper sparrow, Brewer's sparrow, the lark sparrow, the night hawk, the mourning dove, the sagebrush swift lizard, and the black-tailed jack rabbit are present in this association.

CANYON DESERT SCRUB

Toward the western border of the Grand Canyon proper and under the plateau along Kanab Creek is the broad Esplanade that has an area of 64,000 acres (25,900 ha.) covered with a very characteristic vegetation. Counts of the dominant plant, *Coleogyne ramo-*

sissima, showed it to make up 90% of the vegetation on the level areas. Other shrubs were *Yucca baccata, Ephedra torreyana, Quercus wilcoxii, Chrysothamnus* sp. and elephant ears, Opuntia. In the ravines *Fallugia paradoxa,* the most abundant shrub, made up about 60% and *Quercus wilcoxii* comprised near 20% of the shrubs present. *Rhus trilobata* was nearly as abundant as live oak.

The animals here include typical desert rodents, birds, and lizards. The antelope ground squirrel is the most common and uniformly distributed mammal, although the area abounds in both variety and numbers of the smaller rodents.

XI. SUMMARY

The area studied is in northern Arizona between the Grand Canyon of the Colorado and the Arizona-Utah boundary. It is a high block plateau with an area of approximately 1,650 square miles (4,275 square km.) and is included in those portions of the Kaibab National Forest and Grand Canyon National Park occurring north of the Colorado River.

The plateau proper has four major biotic communities: (1) *Picea-Abies-Sciurus fremonti* association of the montane forest climax between 8,200 feet and the plateau summit of 9,200 feet (2,500 to 2,800 m.), (2) the *Pinus brachyptera-Scirurus kaibabensis* association of the montane forest climax between 6,800 and 8,200 feet (2,075 to 2,500 m.), (3) the *Pinus-Juniperus-Neotoma* association of the woodland climax between 5,500 and 6,800 feet (1,675 to 2,075 m.) and (4) the *Stipa-Carex-Thomomys* associes or mountain grassland consisting of small areas above 7,800 feet (2,380 m.). Two major plant associations occur on the border and adjoining the plateau: (1) the short-grass grassland to the east and west and (2) Basin sagebrush to the north and northwest both below 5,500 feet (1,675 m.) and above 4,000 feet (1,220 m.). There are also two minor communities present on the edge of the plateau: canyon desert scrub below 5,000 feet (1,525 m.) located within the Grand Canyon; and a narrow discontinuous belt of oak-brush or Petran chaparral at an average elevation of 6,800 feet (2,075 m.).

The general range, seasonal or year long, of many animals found on the plateau is in agreement with the extensive plant communities. The motility of the animals, however, causes them not to show as definite marks of limitation to communities as do the sessile plant species. The range of the animals within the community is very often dependent upon local and subclimax situations and frequently the majority of mammal and bird species are associated with local conditions. However, the correlation of the plant and animal communities in their spatial relationships and their interdependence justifies their consideration as biotic communities.

The relative equal rank of "formations" (Clements, 1920) for the three mountain forests apparently does not hold in their classification as major biotic communities when a study is made of the influent animal species. There are definite recognizable major differences between the xerophytic piñon-juniper woodland and the montane forests, but there are only minor differences between the yellow pine and spruce-fir on the basis of a study of influent animal species. Each montane forest community has some typical birds and at least one typical abundant mammal. A number of species of importance are present in both communities. On a basis of the consideration of influent animals the two montane forest communities on the Kaibab Plateau should be considered as associational rank and not formational.

The native animals of major influence in the community biotics on this area are large wide ranging mammals as deer, mountain lion and coyote; their presence during the short open season in the higher portion of the plateau and a longer period in the lower borders influences relations within the community more than do the resident animals. Influent animal groups on this area in order of their importance appear to be mammals, birds, insects, and reptiles. This order is believed to apply to the relative importance of the animals under primitive conditions on the same area.

There is a definite physiological rhythm in the animals and their activity associated with change in environmental factors due to elevation. This is shown in the time of abundance and the activity of the different animal species. The adjustment may be carried out by migration, hibernation or inactivity. Invertebrate collections show agreement with seasonal progress at different altitudes as did the early spring maxima of birds. This activity was approximately one day later in each 125 feet of latitude between the piñon-juniper and yellow pine study stations. The annual rhythm of many of the animals appears to be independent of actual climatic conditions, while others show a direct response to such conditions.

In the case of the mule deer, their time of migration both upward and downward on this area is correlated with climatic conditions. The Kaibab deer herd, however, very definitely show in their migration activity responses that cannot be explained on the basis of climatic changes, available food, lack of water, snow depth, or unfavorable terrain. The migration routes and direction appear to be a herd habit or tradition response and there are two major herds, one that migrates east and one west and these consist of several minor herds that return to definite wintering areas in these two general ranges. These definite regular migrations into depleted areas and the unwillingness to visit near-by apparently favorable areas have contributed greatly to the seriousness of the overpopulation problem on the area.

A review of the history of the Kaibab plateau from 1906 to 1940 shows variations in numbers of native animals. There has been a steady increase and sudden decrease in deer numbers; no evident increase in certain animals that have been encouraged by protection as the blue grouse; both increases and decreases in the record of the attractive Kaibab squirrel; a decrease in numbers of animals due to hunting as the case of the mountain lion and the extermination

of the timber wolf from the area; a very marked decrease in the band-tailed pigeon, a protected species; an increase in coyotes and porcupines even with moderate "control" measures and unknown fluctuations in rodents, rabbits, birds, and invertebrates. During the same time there has been a marked decrease in the numbers of domestic livestock and feral horses utilizing the area under a program designed to benefit the deer.

The vegetation of the plateau has been modified greatly by both livestock and deer during historic times. The entire plateau was severely overgrazed in the late 1880's by domestic livestock, severe enough that the general vegetational aspect was apparently changed. The result was that the livestock numbers were reduced because of the lack of forage. During the period of 1915 to 1935 a second but no less severe overgrazing took place on the plateau as a result of an overabundance of deer. Certain forage species as Salix and Rubus hav been almost exterminated by this overgrazing. The growth of young aspen was halted over a period of these 20 years and an ideal winter browse range was overutilized to such an extent that carrying capacity was reduced on large areas to an estimated 5 to 10 percent of original conditions. Killing of a large percentage of browse species on much of the winter range, coupled with curtailment of use by cattle and horses has resulted in a very marked change in the composition of the vegetation on these areas. The grass is favored by the extremely small amount of utilization it receives from deer; the browse species are held in check by the moderate to heavy use they receive, with the result that grass is constituting more and more of the total vegetation.

The recent changes in animal numbers and the marked changes in the vegetation of the Kaibab plateau are evidently due in the main to biotic processes, including man, and have been influenced only in a minor way by climatic conditions. The deer herd was protected from hunting by Indians and white men; there began a program of range improvement by reducing the livestock use of the area, and a very intensive predator control program under government supervision was inaugurated. From 1906 to 1924, 674 mountain lions, 21 timber wolves, and 3,025 coyotes were removed from the area (Figure 5). This resulted in almost extermination of the wolves (a final nine were taken in 1926), it exercised a marked control on lion numbers, and a reported decrease in coyote numbers. (However, following this period, coinciding with the enormous losses of deer on the winter range, a decrease in the intensity of the control operation and the elimination of the wolves, there was an increase in the number of coyotes.)

The discontinuing of hunting and limiting of natural enemies on this almost perfect deer range is believed to have operated jointly in favoring the initial increase in deer numbers. Brooks (1926) has explained the abundance and scarcity of deer in British Columbia as influenced by the occurrence of the mountain lion, and the increase on the Kaibab is believed to have been definitely influenced by limitation of lion numbers as well as the control of other predators.

The number of deer, estimated as 4,000 in 1906, increased to an enormous herd estimated at nearly 100,000 at their peak in 1924. This was an annual accumulative increase of approximately 20 percent over the 18-year period. With these enormous numbers both summer and winter ranges were depleted and available food for the deer was only a fraction of what the range could produce under moderate use. This resulted in a catastrophe. The deer died by the thousands. Extremely few fawns survived during the winters of 1924 to 1928, and this resulted in the composition of the herd becoming top heavy with old deer; the normal mortality of old deer continued, perhaps even increased due to the poor forage condition, but more serious was the fact that no young deer survived to replace the older animals. This would have resulted in an accelerated downward trend in total numbers even in the absence of any removal by hunters.

After an enormous amount of controversy and delay following recognition of the problem, sportsman hunting was first inaugurated in 1924 and 683 deer were killed that year. Hunting has continued each year since that time, with the greatest annual removal in 1930 when 5,033 were killed. These removals from a herd composed of old deer accelerated the downward trend of total numbers but was not the primary cause of controlling numbers of deer on the plateau inasmuch as hunting was not undertaken until after the breaking point had been reached and the "die off" was under way.

XII. APPENDICES

List of Vertebrates

The species listed here by their complete name have been recorded from the Kaibab Plateau. All the amphibians and reptiles and practically all the mammals listed were collected during the period of the study. The list does not include all the vertebrates found in the Grand Canyon bordering the plateau on the south and the surrounding desert areas. The bird list is based on both sight records and collections.

Amphibians and Reptiles

Amphibians

Ambystoma tigrinum (Green)
Tiger Salamander
Scaphiopus hammondii (Baird)
Western Spade-foot Toad

Reptiles

Crotaphytus collaris baileyi Stejneger
Western Collared Lizard
Uta stansburiana stansburiana Baird and Girard
Brown-shouldered Uta
Sceloporus elongatus Stejneger
Stejneger's Blue-bellied Lizard
Sceloporus magister Hallowell
Desert Scaly Lizard
Sceloporus graciosus graciosus Baird and Girard
Sagebrush Swift

Phrynosoma douglasii ornatissimum (Girard)
Girard's Short-horned Horned Toad
Pituophis catenifer deserticola Stejneger
Great Basin Gopher Snake
Lampropeltis pyromelana (Cope)
Arizona King Snake
Thamnophis ordinoides vagrans (Baird and Girard)
Wandering Garter Snake
Crotalus confluentus lutosus Klauber
Great Basin Rattlesnake
Crotalus c. abyssus Klauber
Grand Canyon Rattlesnake

BIRDS

Permanent Residents

Astur atricapillus striatulus Ridgway
Western Goshawk
Accipiter velox velox (Wilson)
Sharp-shinned Hawk
Accipiter cooperi (Bonaparte)
Cooper's Hawk
Buteo borealis calurus Cassin
Western Red-tailed Hawk
Buteo regalis (Gray)
Ferruginous Rough-leg
Aquila chrysaetos canadensis (Linnaeus)
Golden Eagle
Falco mexicanus Schlegel
Prairie Falcon
Dendragapus obscurus obscurus (Say)
Dusky Grouse
Lophortyx gambeli gambeli Gamble
Gambel's Quail
Bubo virginianus ssp.
Horned Owl
**Asio wilsonianus* (Lesson)
Long-eared Owl
Colaptes cafer collaris Vigors
Red-shafted Flicker
Asyndesmus lewis Gray
Lewis's Woodpecker
Dryobates villosus leucothorectis Oberholser
White-breasted Woodpecker
Dryobates pubescens leucurus (Hartlaub)
Batchelder's Woodpecker
Picoides tridactylus dorsalis Baird
Alpine Three-toed Woodpecker
Cyanocitta stelleri diademata (Bonaparte)
Long-crested Jay
Aphelocoma californica woodhousei (Baird)
Woodhouse's Jay
**Corvus corax sinuatus* Wagler
American Raven
Cyanocephalus cyanocephalus (Wied)
Piñon Jay
Nucifraga columbiana (Wilson)
Clark's Nutcracker
Penthestes gambeli gambeli (Ridgway)
Mountain Chickadee
Baeolophus inornatus griseus (Ridgway)
Gray Titmouse
**Psaltriparus minimus plumbeus* (Baird)
Lead-colored Bush-tit
Sitta carolinensis nelsoni Mearns
Rocky Mountain Nuthatch
Sitta canadensis Linnaeus
Red-breasted Nuthatch
Sitta pygmaea melanotis van Rossem
Pygmy Nuthatch
Certhia familiaris montana Ridgway
Rocky Mountain Creeper
Catherpes mexicanus conspersus Ridgway
Canyon Wren
**Salpinctes obsoletus obsoletus* (Say)
Rock Wren
**Turdus migratorius propinquus* Ridgway
Western Robin
**Sialia currucoides* (Bechstein)
Mountain Bluebird
**Carpodacus cassini* Baird
Cassin's Purple Finch
Pinicola enucleator montana Ridgway
Pine Grosbeak
Spinus pinus pinus (Wilson)
Pine Siskin
Loxia curvirostra grinnelli Griscom
Crossbill
**Pipilo maculatus montanus* Swarth
Spurred Towhee
**Junco phaeonotus dorsalis* Henry
Red-backed Junco
**Melospiza melodia fallax* (Baird)
Mountain Song Sparrow

Summer Residents

Cathartes aura septentrionalis Wied
Turkey Vulture
Buteo swainsoni Bonaparte
Swainson's Hawk
Falco sparverius phalaena (Lesson)
Desert Sparrow Hawk
Tringa solitaria cinnamomea (Brewster)
Western Solitary Sandpiper
Columba fasciata fasciata Say
Band-tailed Pigeon
Zenaidura macroura marginella (Woodhouse)
Western Mourning Dove
Phalaenoptilus nuttalli nuttalli (Audubon)
Nuttall's Poor-will
Chordeiles minor ssp.
Night Hawk
Aeronautes saxatalis saxatalis (Woodhouse)
White-throated Swift
Archilochus alexandri (Bouchier and Mulsant)
Black-chinned Hummingbird
Selasphorus platycercus platycercus (Swainson)
Broad-tailed Hummingbird
Selasphorus rufus (Gmelin)
Rufous Hummingbird
Sphyrapicus varius nuchalis Baird
Red-naped Sapsucker
Sphyrapicus thyroideus nataliae (Malherbe)
Natalie's Sapsucker
Myiarchus cinerascens cinerascens (Lawrence)
Ash-throated Flycatcher
Empidonax wrighti Baird
Wright's Flycatcher
Myiochanes richardsoni richardsoni (Swainson)
Western Wood Pewee
Nuttallornis mesoleucus (Lichtenstein)
Olive-sided Flycatcher
Tachycineta thalassina lepida Mearns
Violet-green Swallow
Petrochelidon albifrons albifrons (Rafinesque)
Northern Cliff Swallow
Troglodytes aedon parkmani Audubon
Western House Wren

* Show marked altitudinal migration but are present within portions of the study area year-long.

Oreoscoptes montanus (Townsend)
Sage Thrasher
Hylocichla guttata auduboni (Baird)
Audubon's Hermit Thrush
Sialia mexicana bairdi Ridgway
Chestnut-backed Bluebird
Myadestes townsendi (Audubon)
Townsend's Solitaire
Polioptila caerulea amoenissima Grinnell
Western Gnatcatcher
Corthylio calendula cineraceus (Grinnell)
Western Ruby-crowned Kinglet
Lanius ludovicianus spp.
Shrike
Vireo solitarius plumbeus Coues
Plumbeous Vireo
Vireo gilvus swainsoni Baird
Western Warbling Vireo
Vermivora virginiae (Baird)
Virginia's Warbler
Dendroica auduboni auduboni (Townsend)
Audubon's Warbler
Dendroica nigrescens (Townsend)
Black-throated Gray Warbler
Dendroica graciae graciae Baird
Grace's Warbler
Oporornis tolmiei (Townsend)
Macgillivray's Warbler
Molothrus ater ssp.
Cowbird
Piranga ludoviciana (Wilson)
Western Tanager
Hedymeles melanocephalus papago Oberholser
Rocky Mountain Grosbeak
Passerina amoena (Say)
Lazuli Bunting
Hesperiphona vespertina brooksi Grinnell
Western Evening Grosbeak
Spinus tristis pallidus Mearns
Pale Goldfinch
Spinus psaltria hesperophilus (Oberholser)
Green-backed Goldfinch
Oberholseria chlorura (Audubon)
Green-tailed Towhee
Pooecetes gramineus confinis Baird
Western Vesper Sparrow
Chondestes grammacus strigatus Swainson
Western Lark Sparrow
Amphispiza bilineata deserticola Ridgway
Desert Sparrow
Amphispiza nevadensis nevadensis (Ridgway)
Northern Sage Sparrow
Spizella passerina arizonae Coues
Western Chipping Sparrow
Spizella breweri breweri Cassin
Brewer's Sparrow
Zonotrichia leucophrys leucophrys (Forster)
White-crowned Sparrow
Otocoris alpestris ssp.
Horned Lark

Summer Visitors and Migrants

Ardea herodias treganzai Court
Treganza's Heron
Egretta thula brewsteri Thayer and Bangs
Brewster's Egret
Anas platyrhynchos platyrhynchos Linnaeus
Mallard
Chaulelasmus streperus (Linnaeus)
Gadwall
Dafila acuta tzitzihoa
Pintail
Nyroca sp.
Scaup
Querquedula cyanoptera (Vieillot)
Cinnamon Teal
Querquedula discors (Linnaeus)
Blue Winged Teal
Nettion carolinense (Gmelin)
Green Winged Teal
Circus hudsonius (Linnaeus)
Marsh Hawk
Falco peregrinus anatum Bonaparte
Duck Hawk
Oxyechus vociferus vociferus (Linnaeus)
Killdeer
Actitis macularia (Linnaeus)
Spotted Sandpiper
Catoptrophorus semipalmatus inornatus (Brewster)
Western Willet
Himantopus mexicanus (Miller)
Black-necked Stilt
Steganopus tricolor Vieillot
Wilson's Phalarope
Otus asio ssp.
Screech Owl
Megaceryle alcyon caurina (Grinnell)
Western Belted Kingfisher
Ceophloeus pileatus ssp.
Pileated Woodpecker
Tyrannus verticalis Say
Arkansas Kingbird
Tyrannus vociferans Swainson
Cassin's Kingbird
Sayornis nigricans nigricans (Swainson)
Black Phoebe
Stelgidopteryx ruficollis serripennis (Audubon)
Rough-winged swallow
Regulus satrapa olivaceus Baird
Western Golden-crowned Kinglet
Vermivora celata celata (Say)
Orange-crowned Warbler
Sturnella neglecta Audubon
Western Meadowlark
Xanthocephalus xanthocephalus (Bonaparte)
Yellow-headed Blackbird
Agelaius phoeniceus ssp.
Red-winged Blackbird
Icterus parisorum Bonaparte
Scott's Oriole
Euphagus cyanocephalus (Wagler)
Brewer's Blackbird
Carpodacus mexicanus frontalis (Say)
House Finch

Winter Visitors

Haliaeetus leucocephalus ssp.
Bald Eagle
Pica pica hudsonia (Sabine)
American Magpie
Penthestes atricapillus septentrionalis (Harris)
Long-tailed Chickadee
Bombycilla cedrorum Viellot
Cedar Waxwing
Leucosticte sp.
Rosy Finch

Junco hyemalis hyemalis (Linnaeus)
Slate-colored Junco
Junco oreganus shufeldti Coale
Shufeldt's Junco
Junco mearnsi Ridgway
Pink-sided Junco
Junco caniceps (Woodhouse)
Gray-headed Junco
Zonotrichia leucophrys gambeli (Nuttall)
Gambel's Sparrow

MAMMALS

Eptesicus fuscus fuscus (Beauvois)
Big Brown Bat
Bassariscus astutus nevadensis Miller
Nevada Ringtail
Mustela arizonensis (Mearns)
Arizona Weasel
Spilogale gracilis gracilis Merriam
Little Spotted Skunk
Mephitis estor Merriam
Arizona Skunk
Taxidea taxus berlandieri (Baird)?
Mexican Badger
Urocyon cinereoargenteus scottii (Mearns)
Arizona Gray Fox
Canis lestes Merriam
Mountain Coyote
Canis estor Merriam
Painted Desert Coyote
Felis concolor kaibabensis Nelson and Goldman
Kaibab Mountain Lion
Lynx rufus baileyi Merriam
Plateau Bobcat
Citellus variegatus utah Merriam
Utah Rock Squirrel
Citellus leucurus ssp.
Antelope Ground Squirrel
Citellus lateralis lateralis (Say)
Say's Mantled Ground Squirrel
Eutamias minimus consobrinus (Allen)
Wasatch Chipmunk
Eutamias adsitus Allen
Beaver Mountain Chipmunk
Eutamias dorsalis utahensis Merriam
Utah Cliff Chipmunk
Sciurus kaibabensis Merriam
Kaibab Squirrel
Tamiasciurus fremonti fremonti (Audubon & Bachman)
Fremont Chickaree
Thomomys perpallidus absonus Goldman
Houserock Valley Gopher
Thomomys fossor Allen
Colorado Pocket Gopher
Perognathus longimembris arizonensis Goldman
Little Yellow Pocket Mouse
Perognathus formosus Merriam
Plume-tailed Pocket Mouse
Perognathus intermedius intermedius Merriam
Intermediate Pocket Mouse
Dipodomys ordii cupidensis Goldman
Kaibab Kangaroo Rat
Dipodomys microps leucotis Goldman
Houserock Valley Kangaroo Rat
Onychomys leucogaster melanophrys Merriam
Dark-browed Grasshopper Mouse
Reithrodontomys megalotis megalotis (Baird)
Desert Harvest Mouse
Peromyscus maniculatus rufinus (Merriam)
Tawny White-footed Mouse
Peromyscus maniculatus sonoriensis (LeConte)
Sonora White-footed Mouse
Peromyscus truei truei (Shufeldt)
True's White-footed Mouse
Neotoma lepida monstrabilis Goldman
Kaibab Woodrat
Neotoma cinerea cinerea (Ord)
Colorado Bushy-tailed Woodrat
Microtus mordax mordax Merriam
Rocky Mountain Meadow Mouse
Erethizon epixanthum epixanthum Brandt
Yellow-haired Porcupine
Lepus californicus deserticola (Mearns)
Jack Rabbit
Sylvilagus nuttallii grangeri (Allen)
Black Hills Cottontail
Odocoileus hemionus macrotis Say
Rocky Mountain Mule Deer
Ovis canadensis nelsoni Merriam?
Desert Mountain Sheep

Introduced Mammals

Bison bison bison (Linnaeus)
American Bison

Extirpated Mammals

Euarctos americanus ssp.
Black Bear
Ursus utahensis Merriam?
Grizzly Bear
Canis nubilus nubilus Say
Gray Wolf
Antilocapra americana americana (Ord)
American Antelope

PARTIAL LIST OF INSECTS

Orthoptera

Species collected in quantitative collections and identified by Morgan Hebard.

Oedipodinae

Arphia conspersa Scudder
Camnula pellucida (Scudder)
Trimerotropis cyaneipennis Bruner
Trimerotropis suffusa Scudder
Trimerotropis pallidipennis pallidipennis (Burm.)
Trimerotropis cincta (Thomas)
Trimerotropis inconspicua Bruner
Circotettix coconino Rehn
Melanoplus mexicanus mexicanus (Sauss.)

Rhaphidophorinae

Eremopedes balli Caudell
Oecanthus nigricornis quadripunctatus Beut.

Formicidae

Species collected in quantitative collections and identified by M. R. Smith.
Monomorium minimum Buckley
Crematogaster lineolata (Say)
Pogonomyrmex occidentalis (Cresson)
Myrmica scabrinodis var.
Leptothorax texanus Wheeler
Tapinoma sessile (Say)
Liometopum apiculatum subsp. *luctuosum* Wheeler
Lasius niger var. near *sitkaensis* ? Pergande
Formica fusca var. *subaenescens* Emery

Formica (Proformica) *neogagates lasioides* var. *vetula* Emery
Camponotus sp.
Camponotus herculeanus var. *modoc* Wheeler
Camponotus maculatus vicinus var. *nitidiventris* Emery
Camponotus maculatus vicinus var. *luteangulus* Wheeler

LIST OF PLANTS

This list includes only the names of those plants referred to in the text.

Trees

Pinus edulis Engelm.
Piñon Pine
Pinus brachyptera Engelm.
Rocky Mountain Yellow Pine
Picea pungens Engelm.
Colorado Blue Spruce
Picea engelmanni Parry
Engelmann Spruce
Pseudotsuga taxifolia (LaMarck) Britton
Douglas Fir
Abies concolor Lindley & Gordon
White Fir
Abies lasiocarpa (Hooker) Nuttall
Subalpine Fir
Juniperus communis (L.)
Dwarf Juniper
Juniperus scopulorum Sargent
Rocky Mountain Red Cedar
Juniperus utahensis (Engelm.) Lemmon
Utah Juniper
Populus aurea Tidestrom
Rocky Mountain Quaking Aspen

Shrubs

Ephedra viridis Coville
Mormon Tea
Ephedra torreyana S. Wats.
Torrey Joint Fir
Yucca baccata Torr.
Soapweed
Salix sp.
Willow
Quercus utahensis (A.D.C.) Rydb.
Utah Scrub Oak
Quercus wilcoxii Rydb.
Wilcox Live Oak
Quercus turbinella Greene
Live Oak
Atriplex confertifolia (Torr. & Frem.) S. Wats.
Shadscale
Atriplex canescens (Pursh) Nutt.
Chamise
Eurotia lanata (Pursh) Moq.
Winterfat
Odostemon repens (Lindl.) Cockerell
Oregon Grape
Odostemon fremontii (Torr.) Rydb.
Algerita or Hollygrape
Ribes inebrians Lindl.
Currant
Fallugia paradoxa (Don) Endl.
Apache Plume
Cowania stansburiana Torr.
Cliffrose
Purshia tridentata (Pursh) DC
Bitterbrush
Cercocarpus ledifolius Nutt.
Curlleaf Mountain Mahogany
Cercocarpus intricatus S. Wats.
Small leaf Mountain Mahogany
Rubus sp.
Raspberry
Sericotheca sp.
Ocean Spray
Coleogyne ramosissima Torr.
Blackbush
Amelanchier alnifolia Nutt.
Serviceberry
Robinia neomexicana A. Gray
New Mexico Locust
Rhus trilobata Nutt.
Squawberry
Forsellesia spinescens (A. Gray) Green
Greasebush
Ceanothus fendleri A. Gray
Fendler Ceanothus
Ceanothus greggii A. Gray
Desert Ceanothus
Echinocereus coccineus Engelm.
Hedgehog Cactus
Opuntia tenuispina Engelm.
Elephant-ear Cactus
Opuntia acanthocarpa Engelm. & Bigel.
Stag-horn Cactus
Opuntia basilaris Engelm. & Bigel.
Spineless Cactus
Opuntia polycantha Haworth
Prickly Pear
Opuntia sp.
Cactus
Coryphantha arizonica Engelm.
Pin-cushion Cactus
Arctostaphylos patula Greene
Greenleaf Manzanita
Sambucus coerulea Raf.
Blueberry Elder
Symphoricarpos spp.
Snowberry
Symphoricarpos rotundifolius A. Gray
Round-leaf Snowberry
Gutierrezia sarothrae (Pursh) Britt. & Rusby
Snakeweed
Chrysothamnus spp.
Yellow Brush
Chrysothamnus parryi (Gray) Greene
Rabbit Brush
Artemisia nova A. Nels.
Small Sagebrush
Artemisia tridentata Nutt.
Big Sagebrush

Herbs

Calochortus nuttallii Torr. & Gray
Sego-lily
Razoumofskya cryptopoda (Engelm.) Coville
Yellow Pine Mistletoe
Razoumofskya divaricata (Engelm.) Coville
Piñon Mistletoe
Eriogonum spp.
Wild Buckwheat
Polygonum spp.
Knotweed
Silene douglasii Hooker
Catchfly

Ranunculus alismellus (A. Gray) Green
Buttercup
Ranunculus subsagittatus (A. Gray) Green
Buttercup
Saxifraga rhomboidea Greene
Saxafrage
Potentilla spp.
Cinquefoil
Fragaria platypetala Rydb.
Strawberry
Lupinus spp.
Lupine
Lupinus barbiger S. Wats.
Lupine
Trifolium spp.
Mountain Clover
Lotus wrightii (A. Gray) Green
Red and Yellow Pea
Astragalus spp.
Milk Vetch
Geranium fremontii Torr.
Geranium
Erodium cicutarium (L.) L'Her.
Filaree
Sphaeralcea marginata York
Globemallow
Pseudocymopterus montanus (A. Gray) Coulter & Rose
Wild Carrot
Pyrola secunda L.
Shinleaf
Pyrola picta Smith
Shinleaf
Phlox caespitosa Nutt.
Phlox
Gilia spp.
Gilia
Oreocarya spp.
Beggar Lice
Pentstemon spp.
Pentstemon
Castilleja spp.
Paintbrush
Castilleja pinetorum Fernald
Yellow Pine Paintbrush
Orthocarpus luteus Nutt.
Yellow Owl's Clover
Orthocarpus purpureo-albus A. Gray
Orthocarp
Linnaea borealis americana (Forbes) Rehder
Twin Flower
Campanula parryi A. Gray
Hairbell
Solidago sp.
Goldenrod
Aster spp.
Aster
Erigeron spp.
Daisy
Erigeron divergens Torr. & Gray
Daisy
Solidago petradoria Blake
Goldenrod
Antennaria spp.
Pussytoes
Hymenopappus lugens Greene
Hymenopappus
Actinea spp.
Pingue or Rubberweed
Artemisia gnaphalodes Nutt.
Cudweed Sage
Artemisia forwoodii S. Wats.
Herbaceous Sage
Artemisia mexicana Willd.
Sweet Sage
Leontodon taraxacum L.
Common Dandelion
Agoseris sp.
Mountain Dandelion
Achillea lanulosa Nutt.
Yarrow

Grasses and Grasslike Plants

Hilaria jamesii (Torr.) Benth.
Galleta Grass
Stipa comata Trin. & Rupr.
Needle and Thread Grass
Oryzopsis hymenoides (Roem. & Shult.) Ricker
Rice Grass
Muhlenbergia sp.
Muhly
Muhlenbergia montana (Nutt.) Hitchc.
Mountain Muhly
Phleum alpinum L.
Mountain Timothy
Sporobolus cryptandrus (Torr.) A. Gray
Sand Dropseed
Blepharoneuron tricholepis (Torr.) Nash
Hairy Dropseed
Deschampsia caespitosa (L.) Beauv.
Hairgrass
Koeleria cristata (L.) Pers.
Junegrass
Bouteloua gracilis (H. B. K.) Lag.
Blue Grama Grass
Bouteloua rothrockii Vasey
Crowfoot Grama
Bouteloua eriopoda Torr.
Black Grama
Bouteloua curtipendula (Michx.) Torr.
Side-oats Grama
Munroa squarrosa (Nutt.) Torr.
False Buffalo Grass
Scleropogon sp.
Burro Grass
Poa spp.
Blue Grass
Festuca spp.
Fescue
Bromus porteri Coulter
Bromegrass
Sitanion hystrix (Nutt.) J. G. Smith
Bottlebrush Squirreltail
Carex spp.
Sedge

XIII. LITERATURE CITED

Bailey, F. M. 1928. Birds of New Mexico. New Mex. Dept. of Game and Fish. Santa Fe. 1-807.

Bird, R. D. 1929. Biotic communities of the aspen parkland of central Canada. Ecology **11**: 356-442.

Blake, I. H. 1926. A comparison of the animal communities of coniferous and deciduous forests. Ill. Biol. Monogr. **10**: 371-520.

Brooks, A. 1926. Past and present big game conditions in British Columbia and the predatory mammal question. Jour. Mammal. **7**: 37-40.

Clements, F. E. 1916. Plant succession: An analysis of the development of vegetation. Carnegie Inst. Wash. Pub. 242.

———. 1920. Plant indicators: The relation of plant communities to process and practice. Carnegie Inst. Wash, Pub. 290.

Clepper, H. E. 1931. The deer problem in the forests of Pennsylvania. Pa. Dept. Forests and Waters Bull. **50**: 1-45.

Dayton, W. S. 1931. Important western browse plants. U. S. Dept. Agri. Misc. Pub. **101**: 1-214.

Dice, L. R. 1930. Methods of indicating relative abundance of birds. The Auk. **47**: 22-24.

Dutton, C. E. 1882. The physical geology of the Grand Canyon district. 2nd Ann. Rep. U. S. Geol. Surv., 1880 and 1881. Washington. 49-293.

Goldman, E. A., and S. B. Locke. 1923. The mountain of twenty thousand deer. Amer. Forestry **29**: 649-653; 682.

Grinnell, J. 1924. Wild animal life as a product and as a necessity of national forests. Jour. of For. **22**: 837-845.

———**, and T. I. Storer.** 1924. Animal life in the Yosemite: An account of the mammals, birds, reptiles, and amphibians in a cross-section of the Sierra Nevada. Univ. Calif. Press. Berkeley. 1-752.

Hall, E. R. 1925. Report on the Kaibab deer. Unpublished memorandum. U. S. Biological Survey files.

Hanson, H. C. 1924. A study of the vegetation of northeastern Arizona. Univ. Nebr. Studies **24**: 1-94.

Hough, E. 1922. The president's forest. Sat. Eve. Post. **194**: 6-7 + Jan. 14; 23 + Jan. 21.

King, K. M. 1927. A quantitative investigation of the fauna of native and ruderal associations at Saskatoon, Saskatchewan, with special reference to climatic influences. Abstract. Bull. Ecol. Soc. Amer. **8**(4): 5.

Mann, W. G., and S. B. Locke. 1931. The Kaibab deer: A brief history and recent developments. Mimeographed. U. S. Forest Service. 1-70.

Mead, P. 1930. An ecological description of the Kaibab Plateau, Arizona. Unpublished Master's Thesis, Univ. of Chicago.

Merriam, C. H. 1890. Results of a biological survey of the San Francisco Mountain Region and the desert of the little Colorado, Arizona. North American Fauna 3.

Pearson, G. A. 1920. Factors controlling the distribution of forest types. Ecology **1**: 139-159; 289-308.

Pearson, T. G. 1925. The deer of the Kaibab. Nat. Mag. **5**: 158-160.

Powell, J. W. 1875. Exploration of the Colorado River of the west and its tributaries. Govt. Printing Office. Washington. 1-291.

Russell, C. P. 1932. Seasonal migration of mule deer. Ecol. Monogr. **2**: 1-46.

Shackleford, M. W. 1929. Animal communities of an Illinois prairie. Ecology **10**: 126-154.

Shelford, V. E. 1913. Animal communities in temperate America. Chicago. 1-362.

———. 1926. Terms and concepts in animal ecology. Ecology **7**: 389.

———. 1930. Ways and means of improving the quality of investigations and publications in animal ecology. Ecology **11**: 235-237.

Shiras, G., III. 1924. The mule deer of the Kaibab National Game Preserve. Unpublished memorandum. Kaibab National Forest files.

Shreve, F. 1917. A map of the vegetation of the United States. Geog. Rev. **3**: 119.

Smith, V. G. 1928. Animal communities of a deciduous forest succession. Ecology **9**: 479-500.

Taylor, W. P. 1930. Outlines for studies of mammalian life-histories. U. S. Dept. Agri. Misc. Pub. **86**: 1-12.

United States Forest Service. 1905-39. Annual grazing reports of forest supervisor, Kaibab National Forest. Unpublished.

———. 1905-39. Annual game reports of forest supervisor, Kaibab National Forest. Unpublished.

———. 1924. The report of the Kaibab investigative committee appointed by the U. S. Secretary of Agriculture. Unpublished.

———. 1928. The decision of the United States Supreme Court concerning the deer of the Kaibab National Forest. Kaibab National Forest files.

———. 1931. Kaibab investigative committee, June 8 to 15, 1931. (Report of committee appointed by the U. S. Secretary of Agriculture.) Mimeographed. 1-11.

United States Weather Bureau. 1920-38. Summary of the climatological data for the U. S. by sections. Section 4, Northern Ariz. Govt. Printing Office. Washington.

Vestal, A. G. 1913. An associational study of Illinois sand prairie. Bull. Ill. State Lab. Nat. Hist. **10**: 1-96.

Vorhies, C. T., and W. P. Taylor. 1933. The life histories and ecology of jack rabbits. *Lepus alleni* and *Lepus californicus* sp. in relation to grazing in Arizona. Univ. Ariz. Agri. Exp. Sta. Tech. Bull. **49**: 467-587.

Weaver, J. E., and F. E. Clements. 1929. Plant ecology. New York. 1-520.

Weese, A. O. 1924. Animal ecology of an Illinois elm-maple forest. Ill. Biol. Monogr. **9**: 345-438.

PRIMARY SUCCESSION ON VOLCANIC DEPOSITS IN SOUTHERN IDAHO

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PRIMARY SUCCESSION ON VOLCANIC DEPOSITS IN SOUTHERN IDAHO

INTRODUCTION

Some of the most recent volcanic deposits to be found within the United States are in that portion of Idaho known as the Snake River plains, or, as sometimes improperly called, the Snake River desert. Because the term "plains" is in common usage it is retained in this discussion, but the character of the region is such that "plateau" would be more descriptive. The plain has been built up by volcanic outpourings and has an elevation of from 3,000 to 6,000 feet, being highest in the north-central and eastern parts. The region is nearly surrounded by mountains. These are almost unbroken at the north and east; to the south there are north-south trending ranges. Mountains are fewer in the west where the plains merge with the Columbia Plateau. The length of the region is about 350 miles; the width varies between approximately 50 and 75 miles. An otherwise regular topography is broken by numerous volcanic cones; the largest, Big Butte, southeast of Arco (Fig. 1), rises 2,350 feet above the surrounding area (Russell, 1902). Near by are the smaller Twin Buttes (Fig. 1); elsewhere there are smaller cones. The Snake River flows westward across the entire length of the plains. Its northern tributaries are few, even though there are vast mountain areas in which streams rise. Most of these streams disappear from sight and become "lost rivers" shortly after they reach the lava plains, owing to the porosity of the flows and the thinness of the soil mantle overlying them.

White men have known of the Snake River plains since 1810, when Wilson Price Hunt and his party crossed them on their way to the Columbia River (Irving, 1839). Within a few years the plains became a part of a regular highway for trappers and traders. Soon the region was traversed also by settlers who were following the Oregon Trail. For all people the trip across the plains was a difficult one; the Snake River was too turbulent to permit the use of boats and a shortage of water and game made the journey by land trying.

Settlement of the plains was begun in 1834 when Old Fort Hall was built near the Snake River in the eastern part. By 1854, when the Mormons are reported to have brought cattle to the Salmon River (Brosnan, 1935), grazing was probably established on a permanent basis in the region. It has continued to be the chief occupation of inhabitants over much of

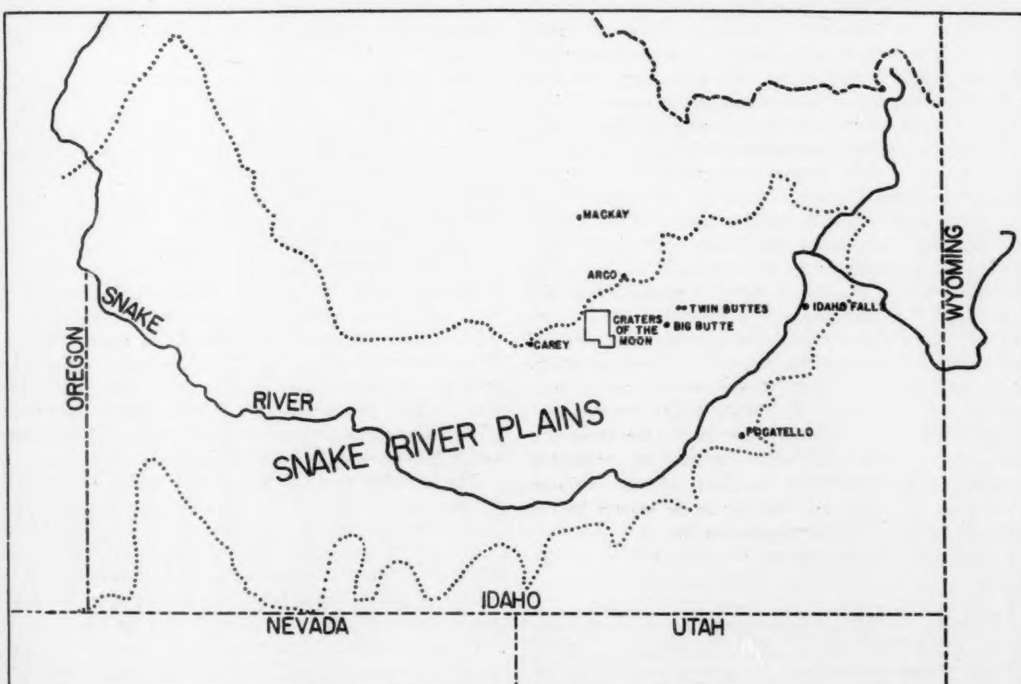

FIG. 1. Snake River plains and adjoining region.

the region, except in relatively small areas, chiefly near the Snake River, where water is available for irrigation, and in areas too rough and unproductive for grazing use, such as the one specifically discussed in this paper.

Sage *(Artemisia tridentata)*,[1] is the dominant plant species over most of the plains. In addition other shrubs, as well as grasses and other herbs, occur. In limited areas trees make up a part of the vegetation. Junipers (*Juniperus scopulorum* and *J. utahensis*) occur in some places, and, more rarely, Douglas fir *(Pseudotsuga taxifolia)*. Most important of the trees is limber pine *(Pinus flexilis)*. The trees are found mainly in an area about 15 miles north and south by 50 miles east and west, lying between Big Butte and Twin Buttes on the east and the town of Carey on the west (Fig. 1).

The earliest available records giving information on vegetation of the plains are those of Captain Bonneville (Irving, 1843), who was in the region during the years 1832 to 1835. It is quite evident that sage was an important member of the vegetation at that time; grass was abundant near streams but not elsewhere. The next vegetation record is that of Israel C. Russell (1902) who did geologic work on the plains in 1901. He reported sage as the characteristic plant, with bunch-grasses between the sage bushes. His description applies in general today. Sage is and evidently has been a dominant member of the vegetation since the advent of the first white men into the region.

It is possible that vegetation disturbance has not been much greater since the coming of the white man than it was before. Grazing has undoubtedly increased, although the Indians had horses, and at times each year there were buffaloes in abundance (Irving, 1843). Fires have probably decreased. Bonneville reported that at certain seasons the sky was darkened for days at a time by smoke from fires set by the Indians (Irving, 1843).

The vegetation which occupies most of the Snake River plains has become established under the conditions of disturbance just mentioned. What effect the disturbance has had upon the character of the vegetation is not known. It may be that if fires and grazing were entirely eliminated for a number of years changes would occur in the floristic composition, or at least in the relative abundance of species now present. Weaver and Clements (1929) suggest that if the Snake River plains were kept free from fire and grazing they would come in time to support a grassland climax, similar to that of the Palouse Prairie in Washington. So far as is known to the writer, Palouse Prairie vegetation has not been adequately demonstrated to be the climax type in the Snake River region. The writer has seen only one instance where an area not within the protecting influence of a cone, or near a stream, has a nearly pure grass stand. Two small kipoukas,[2] each less than ⅛ mile in diameter, located in the north-central part of the region, support vegetation of the type shown in Figure 2. These kipoukas are surrounded on all sides

FIG. 2. A kipouka surrounded by young lava flows. The predominant vegetation is bunch-grass; shrubs, though not absent, are small. Crater wall fragment in the distance. August 1, 1938.

by over a mile of fresh lava and have probably never been grazed, but one of them gave indication of having been partly burned recently. Although the evidence given here seems to confirm the opinion offered by Weaver and Clements (1929), it is not believed that one such instance is sufficient to warrant application to an entire region. Therefore, it is tentatively assumed that the grass-sage type of vegetation, which now occupies, and has occupied as far back as is known, most of the Snake River plains, is the regional climax.

One of the most interesting sections of the plains, from a botanical viewpoint, lies in the north-central part. In that area recent volcanic activity has occurred, some possibly less than a thousand years ago. It is there that trees occur in greatest numbers and that most variation exists in the vegetation of closely adjacent areas. Many parts have not been subjected to grazing because they are surrounded by fresh lava fields; the kipoukas mentioned above are an example. The major part of the region where the most recent volcanic activity took place lies within the Craters of the Moon National Monument, an area of about 75 square miles (Fig. 1). The Monument lies at the extreme northern edge of the plains, and is at the very foot of the mountains. The elevation over most of the Monument is between 5,300 and 6,000 feet; one tall volcanic cone rises to 6,515 feet above sea level.

The greater part of this study, which deals with primary succession on the volcanic material, was carried on within or not over two miles outside of the National Monument. Several reconnaissance trips were made into the surrounding country, within a radius of about 30 miles. The field work was done during the summers of 1936 to 1938, inclusive.

I wish to thank Professor W. S. Cooper and Dr. D. B. Lawrence of the University of Minnesota for

[1] Nomenclature of grasses follows Hitchcock (1935); that of trees, Sargent (1921); and that of shrubs, and herbs other than grasses, is according to Coulter and Nelson (1909), or Rydberg (1917), except in a few instances where neither manual describes a species, or when more recent work suggests a preferable name. Specimens of all species have been placed in the herbarium of the Botany Department of the University of Minnesota.

[2] A kipouka, sometimes spelled kipuka (Verhoogen, 1937) is an island of old rock surrounded by young.

their assistance in the furtherance of this work. Especially valuable suggestions were obtained from the latter when he spent several days in the field in the summer of 1938 while the investigation was in progress; he has also offered helpful criticisms during the preparation of the manuscript. My wife, Dorothy S. Eggler, was my co-worker in the field. To former custodian A. T. Bicknell and present custodian G. E. McCarty of the Monument I extend my sincere appreciation for their interest and kindness.

CLIMATIC RELATIONS

The climate of the Snake River plains may in general be described as mid-continental in character, having scanty precipitation, rather cold winters and hot summers.

No long-time climatic data are available for the Monument itself, but it is believed that the use of records from the nearest stations of the Snake River plains is permissible, and that these give a fairly accurate picture of the weather conditions in the Monument. Records from the United States Weather Bureau stations at Aberdeen, Arco, Idaho Falls, Mackay, and Pocatello (Fig. 1) are introduced in the following report. Mackay is the only one of those stations not on the Snake River plains proper; it is in a tributary valley and the climate is quite similar to that of the Monument. Conditions at Arco, 18 miles east of the Monument, at about the same elevation, probably most nearly approximate those of the Monument. Wherever pertinent, my own observations made within the study area are added to supplement the long-time records.

PRECIPITATION

Over the region as a whole less than 40 percent of the annual precipitation of under 14 inches falls during the frostless season; at Arco less than 27 percent during that period. There are two periods of relatively high precipitation during the year, December and January, the time of greatest snowfall, and May and June, the time of maximum rainfall (Fig. 3).

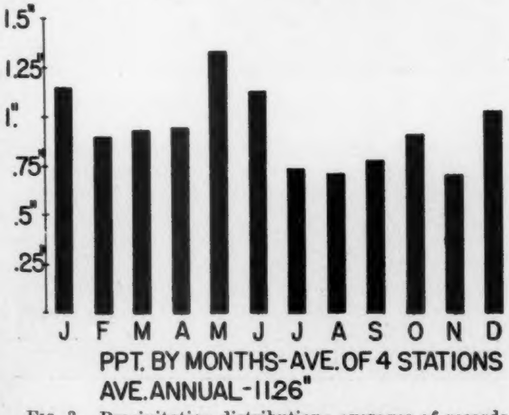

FIG. 3. Precipitation distribution; averages of records from Arco, Idaho Falls, Mackay, and Pocatello.

Some years there may be no precipitation during one or more months from July to September (U. S. Weather Bur. Bull. W, 1926). At Arco slightly less than half the precipitation falls as snow—4.28 inches of the total of 9.63 per year.

TEMPERATURE

Normal temperature records (Table 1) show winters to be moderately cold and summers moderately hot. The extremes which have been registered at Arco are –41° F. in February and 101° F. in July. The mean maximum for July, the hottest month, is 82.5 ° F.; the mean minimum for January, the coldest month, 1.8° F. Killing frosts may occur any month of the year; they have been recorded on July 18 and on August 18 (U. S. Weather Bur. Bull. W, 1926). Records for Pocatello were obtained directly from the station office; those for other stations from the Weather Bureau office at Boise, Idaho.

TABLE 1. Climatic data.

	January	February	March	April	May	June	July	August	September	October	November	December	Annual
Arco	14	20	30	43	51	57	66	64	55	44	31	18	41.2
Idaho Falls	20	25	35	45	53	61	69	65	57	47	34	22	44.4
Mackay	17	21	31	42	51	59	67	65	55	45	32	20	42.1
Pocatello	24	29	37	46	54	62	71	70	60	48	37	27	47.1

	Period of Record Precip.	*Period of Record* Temp.	*Elevation*	*Distance and Direction from the Monument*
Arco	31 yrs.	25 yrs.	5,318 feet	18 miles—East
Idaho Falls	41 yrs.	28 yrs.	4,742 feet	83 miles—East
Mackay	25 yrs.	24 yrs.	5,897 feet	55 miles—Northeast
Pocatello	39 yrs.	39 yrs.	4,477 feet	90 miles—Southeast

As is characteristic of semi-arid plateaus the nights are cool and the days warm in summer. Summer skies are clear, and there is no extensive cloud blanket to retard the rates of insolation and reradiation of heat. With such conditions rapid temperature changes are characteristic.

Air temperature measurements were made in the study area by means of a shaded thermograph during the period of June 17 to August 1, 1938. The maximum daily temperature was generally reached between two and four in the afternoon, the minimum between four and six in the morning. The highest temperature recorded during the period was 97.5° F., on July 22; the minimum, 25° F., on June 19. These two days exhibited the characteristically great daily temperature ranges of summer. At six o'clock in the morning on the day the maximum of 97.5° was attained the temperature was 48 degrees; the range for the day was 49.5° F. On the afternoon of the day when the 25° minimum was reached the temperature rose to 76.5° F., a range of 51.5° for the day. The average daily range during the June period was 38.2° F., during July 39.1° F.

Plants growing under these conditions must withstand what would seem to be a rather serious shock to their protoplasm twice a day, and this feature of the climate may play some part in determining the distribution of plants in this region.

WIND

Southwest winds prevail over the Snake River plains much of the time; at Arco it is the prevailing direction all months of the year.

At Pocatello, the nearest Weather Bureau station at which wind velocity measurements are made, the average hourly movement is 8.8 miles. The velocity is quite uniform during all months of the year (U. S. Weather Bur. Bull. W, 1926).

In the Monument, on a typical summer day, the wind usually rises during the morning and by noon or shortly after it often reaches a velocity of 15 to 20 miles an hour in unprotected places. Rarely it attains a velocity of 32 to 38 miles per hour, as estimated by the Beaufort Scale of wind force. The wind almost always dies down in late afternoon, and is quiet by sundown; nights are usually calm.

PRECIPITATION-EVAPORATION RATIO

The concept of a precipitation-evaporation ratio to express plant water relations has been used widely and has undergone several modifications since first employed by Transeau (1905). Transeau obtained the P/E ratio by dividing normal annual precipitation by the total evaporation record of a single year; on this basis he worked out climatic zones for the eastern United States. Annual evaporation data for Snake River plains stations are not available, so it is not now possible to compare the region with Transeau's climatic zones. P/E ratios are useful here as a means of comparing the moisture conditions among the months for which data are available. Such ratios are more useful than precipitation alone in that they give a measure of the water balance with which a plant has to work.

Records for calculating the P/E ratio were obtained for the months of April through September, 1914 to 1919, inclusive, from Aberdeen, Idaho, which is the only station in the region at which both evaporation and precipitation records have been made (Horton, 1921; U. S. Weather Bur. Bull. W, 1926). Aberdeen is about 50 miles southeast of the Monument, at an elevation of 4,400 feet. Amount of precipitation and seasonal distribution there are quite similar to those at Arco. P/E ratios are given in Table 2.

TABLE 2. P/E ratios computed for Aberdeen, Idaho.

	April	May	June	July	Aug.	Sept.
1914	0.150	0.074	0.380	0.058	0.000	0.243
1915	0.113	0.444	0.066	0.060	0.016	0.268
1916	0.073	0.212	0.009	0.049	0.048	0.000
1917	0.432	0.632	0.022	0.032	0.002	0.048
1918	0.118	0.073	0.108	0.174	0.055	0.208
1919	0.135	0.034	0.000	0.044	0.018	0.363
Average	0.170	0.245	0.198	0.070	0.023	0.190

May has definitely the most favorable moisture conditions for plant growth, and August the least. Despite the good moisture conditions in May it is probable that it is then too cold for best growth because freezing weather is common. June normally has no freezing weather after the first week, but already moisture conditions are becoming less satisfactory. It is probably the best month for growth because the moisture-temperature combination is nearest an optimum.

CHEMICAL AND PHYSICAL CHARACTER OF LAVA AND CINDERS

The plains character of the Snake River country is due largely to the manner of accumulation of volcanic material and little to subsequent erosion. Vents have supplied material in many places over a long period of time, from Miocene to Recent (Russell, 1902) and the surface in the large is nearly level. The youngest lava within the boundaries of the Monument is believed to be "more than 250 years but perhaps not more than 1,000" in age (Stearns, 1930) and it still retains an unweathered appearance. All volcanic material exposed at the surface within the Monument is basaltic in nature, as is the more recent over all the plains, and as a result there should be marked chemical uniformity in the various deposits regardless of their physical characteristics. The volcanic ejecta occur chiefly as two types, flows and cinders. Flows are essentially solidified lava streams. Individual flows range in area from a few acres to a few square miles. Within the Monument there are about 30 flow exposures, varying in age, degree of weathering, and amount and kind of vegetation.

The flows are of two types: (a) a broken, jagged, fragmental kind, known as "aa" (Fig. 4), and (b) a smoother, ropy or billowly type called "pahoehoe," which is generally somewhat cracked and fractured (Fig. 5).

The area occupied by cinders is small in comparison to that covered by the flows. Cinders are massed in

FIG. 4. An aa lava flow. August 22, 1938.

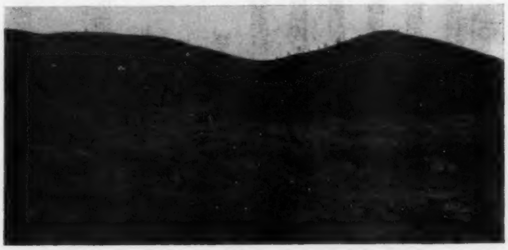

FIG. 5. North Crater Flow, a pahoehoe flow. August 27, 1938.

cinder cones, which are, according to Stearns (1930), "heaps of lava froth or spray formed by the fire fountains which played at the time of the eruptions." There are about 35 distinct accumulations in the Monument, ranging in height above the surrounding lava from approximately 50 to 800 feet, with basal diameters up to a mile. A majority of these cones are aligned in a zone with a northwest-southeast trend (Fig. 6), which has been given the name "The Great

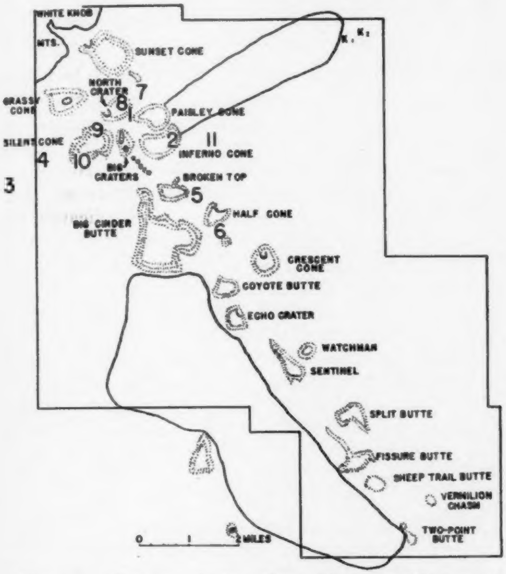

FIG. 6. Craters of the Moon National Monument. Cinder cones are aligned in a zone, the "Great Rift." Between the cones, and at the sides, are flows. Enclosing lines mark the locations of regions of good tree growth. Numbers mark the sites of detailed studies.

Rift." This zone has been the scene of great volcanic activity and was the source of most of the lava flows of the Monument, as well as the cones. Like the flows, the cinder cones vary in age and hence in degree of weathering and in vegetation.

PAHOEHOE LAVA FLOWS AND THEIR VEGETATION

GROWTH CONDITIONS ON FLOWS

GENERAL FEATURES

The 30 or more lava flows which are entirely or partly within the Monument represent together an age span of several thousands of years, and upon them can be found vegetation representing all the stages of primary succession from pioneer to the regional climax. Some flows are extremely fresh in appearance in that *superficially* neither soil nor vegetation is visible. Closer examination shows, however, that even the youngest flows have some soil present in depressions and that in these a few vascular plants are becoming established; only scattered lichens grow on the general flow surface. Other flows show their great age by being almost completely mantled with soil and vegetation, and only here and there does the bare lava protrude. Between the two extremes in age are flows which are partly soil-covered but which have a considerable amount of bare lava exposed. These are intermediate also in the character of their vegetation.

FOUR VEGETATION HABITATS OF YOUNG FLOWS AND HOW THEY CHANGE AS FLOW AGE INCREASES

A young pahoehoe flow is of such character that it presents four types of habitat. Each is sufficiently distinctive in growing conditions it provides that it is invaded by a definite set of plants. Succession beginning in each habitat type will be considered as a subsuccession of the whole.

The habitat which occupies the greater part of a young pahoehoe flow is the nearly level lava surface. Here growing conditions are unfavorable; water runs off almost immediately; the surface is openly exposed to wind and sun. Soil accumulates very slowly, and it is only after all crevices and depressions are filled that wind-blown soil collects on the flow surface. It therefore continues as a xeric habitat without much improvement in growing conditions until late in the process of succession.

The other three habitats are forms of crevices or depressions in the flow, and their subdivision is based on depth and width of the crevice. They are here given the descriptive names "joint," "shallow crevice," and "deep crevice." Joints are too narrow to hold much soil, so moisture conditions, at least near the surface, cannot be very good. When the flow surface about them becomes soil-covered they too are covered and pass out of existence as a distinct habitat. Until that time in the life of the flow it seems unlikely that growth conditions in joints would change much.

A shallow crevice is any depression of sufficient depth to permit soil to accumulate to a thickness of an inch or more but not deep enough to enable a mature shrub to grow with most of its aerial portion below the general flow surface. A depression of the latter character is here considered a deep crevice. A depth of about 2 feet is usually the dividing point between deep and shallow crevices but it varies somewhat with the steepness of the walls. Deep crevices generally have steep sides, consequently soil does not blow out easily, but accumulates. They are usually fissures in the flow. Shallow crevices may be fissures but are more often depressions between folds or "ropes" of pahoehoe flow where a little soil can lodge (Fig. 7).

Conditions in shallow crevices are probably intermediate, in relation to moisture, between those in deep crevices and the flow surface. There is concentration of precipitation in them, but being open to exposure, water loss by evaporation is rapid. Shallow crevices usually do not have soil to a depth of over 2 or 3 inches, and so the soil-water reservoir is small. The fate of shallow crevices is to be leveled with soil, but usually not until the deep ones are first nearly filled.

Moisture conditions in deep crevices are the most

favorable to be found in any of the four habitats of young flows. Deep crevices provide the best lodging place for both organic and inorganic soil, so they tend to fill rapidly. Addition of soil would improve moisture conditions by increasing the water reservoir. However, the value of the increased soil layer is offset as soon as the accumulation is sufficient to raise the aerial parts of plants above the general flow surface; then water loss from plants becomes too great for their survival. The nearer the crevice soil approaches the flow surface the more it is desiccated. In this way the deep-crevice habitat gradually ceases to exist as flow age increases.

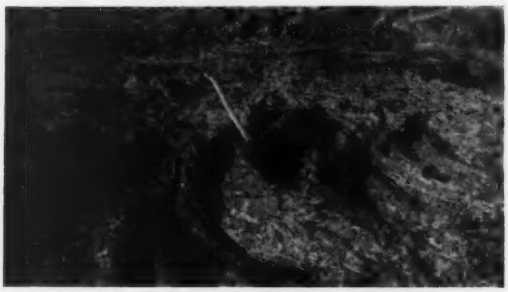

FIG. 7. Very ropy lava of Indian Tunnel Flow. Soil has accumulated in depressions and pioneer plants have started. August 1, 1938.

FLOW SOILS

It has been found that the amount of soil on a flow is the most important single factor in determining the vegetation a flow can support. Therefore a consideration of flow soils is necessary before the development of the vegetation can logically be discussed.

These soils are fine in texture, and, according to Russell (1902), are mostly wind-transported, the sources being alluvial deposits near the mountain bases, ancient lacustrine beds in the western part of the plains, and dust and lapilli from cinder cones. He called the soil loess. Mechanical analyses of three samples taken at widely separated places on the Snake River plains, each at a foot depth, were made by him. The materials of all samples were found to be predominantly quartz and of uniformly fine texture, 75 to 80 percent of soil passing through a screen with 200 meshes per inch.

In the present work three samples of surface soils were taken from locations where the accumulation is thin. One site was an old flow about 5 miles east of Carey, and 22 miles west of the Monument, where the soil layer was approximately 6 inches thick; another was Silent Cone Flow, at Station 3 (Fig. 6), where the layer varies from 0 to 2 feet in depth; the third was from crevices in the young flow between Half Cone and Crescent Butte (Station 6, Fig. 6), and thus represents the first soil found on a flow.

Mechanical analyses of these soils (Table 3) showed them to be, in general, as fine in texture as were Russell's. Nearly three-fourths of the material in each sample was small enough to have been wind-

TABLE 3. Textures of three soils, as determined by mechanical analyses; values expressed in percentages.

	Surface of old flow east of Carey	Crevice in flow between Half Cone and Crescent Butte	Surface Silent Cone Flow
2 – 1 mm.....	6.42	2.11	5.08
1 – .5 mm.....	1.78	3.23	2.04
.5 – .25 mm.....	1.87	5.01	3.24
.25– .1 mm.....	6.38	18.90	12.38
.1 – .05 mm.....	14.59	22.76	16.88
Less than .05......	68.95	47.98	60.38

blown. The crevice material was slightly less fine than the other two, suggesting a colluvial origin, at least in part. Pieces of angular basalt, products of mechanical weathering of the flows, made up about 25 percent of the crevice soil; other soils contained less. The pieces ranged in diameter up to an inch or two. Nearly all those observed gave indication of having undergone some chemical weathering.

Microscopic examination of a sample failed to reveal the presence of diatoms, which should be found in a lacustrine deposit. The soil particles were angular in shape and looked like volcanic ash. Examination of many samples, taken at various places on the Snake River plains, would be necessary before it could be said that lake material is unimportant as a soil source in this region, but this one sample is suggestive.

FATE OF PRECIPITATION

The distribution of precipitation which falls upon a young lava flow has a marked influence on the distribution of its vegetation. There is no surface runoff, and, except for what evaporates, all water sinks downward into cracks and crevices. Thus there is an unequal distribution of water, which favors plants growing in crevices at the expense of those not so favorably located.

It is not known if a similar concentration of water would be found on old, soil-covered flows, but, since the lava surface under the soil retains much of its original pahoehoe character, it is likely that water in passing downward must tend to move toward the depressions, when once it has reached the impervious layer. As the thickness of the soil mantle increases, less and less of the precipitation would be expected to reach the rock surface, so that the distribution of moisture must become more and more uniform as a flow increases in age.

A phenomenon which suggests a source of water for certain flow plants is the presence of water, at 33 to 35° F., in numerous depressions and catch-basins on younger flows, during a part or all of the summer. Stearns (1930) discusses the source of this water as follows: "In these depressions a considerable amount of snow collects in winter. Some of it sifts down into crevices between the rocks and remains sheltered from the hot atmosphere during the long summer days. In addition, water during thawing periods in autumn or spring may drip downward into the crevices, where it is frozen by cold circulating air.

During the long cold winters ice forms. Some of it melts in summer, but in favored locations it never melts entirely away. Just as the solid lava is a poor conductor for the upward movement of heat from the molten lava beneath, so it is a poor conductor for the downward passage of heat from the sun. Usually a small amount of ice melts during the summer and forms a pool of water. On digging down into the loose rock in a water hole of this type, ice will always be found beneath the water." It is possible that water from melting ice in cracks may be available to certain deep-crevice plants growing on young flows, or those with roots in joints, but this point has not been verified.

TEMPERATURE AND EVAPORATION ON FLOWS

Not only is precipitation concentrated in cracks but temperature and wind conditions are such that evaporation from crevice floors is much less rapid than from the general flow surface.

To obtain a measure of atmospheric conditions in crevices, as contrasted with those in exposed places, temperature and evaporation measurements were made. An air-soil thermograph was placed on North Crater Flow, with the brass-colored bimetal air element 3½ inches above the general flow surface and not shaded in any way, and the soil element laid on the floor of a deep crevice. The crevice was 31 inches deep, 10 inches wide at the top and three inches wide at the bottom. Weekly records were kept for the period from August 1 to September 5, 1938. The temperature range was found to be greater and changes more rapid just above the flow surface. The temperature there was about 30 degrees higher at the daily maximum and 10 degrees lower at the minimum. Figure 8 gives a typical week's record.

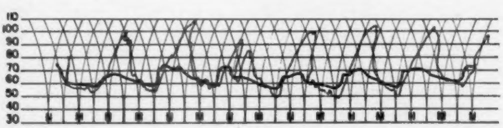

FIG. 8. Thermograph record for a typical week during the period Aug. 1 to Sept. 5, 1938. Narrow line—temperature 3½ inches above the surface of North Crater Flow; wide line—temperature at the bottom of an adjacent 31-inch crevice. N = noon, M = midnight.

During the period from August 6 to 27, 1938, comparative evaporation measurements were made in this same crevice and above the surfaces of two other flows of the Monument. One Livingston white spherical porous-cup atmometer was placed in the crevice, the bulb being 10 inches below the general flow surface. Two similar atmometers were placed on each of the other two flows during the same period, the bulbs being 17 inches above the surface. Comparison of evaporation in the crevice with that at the surface immediately above would have been preferable, but was not possible with the available equipment. It is believed the surface evaporation on North Crater would have been essentially the same as on the two flows where measurements were made.

Figure 9 gives a comparison of evaporation during the three weeks' period in the crevice and above the surfaces. It can be seen that the rate of evaporation 10 inches below the surface was about half that 17 inches above, for the same period.

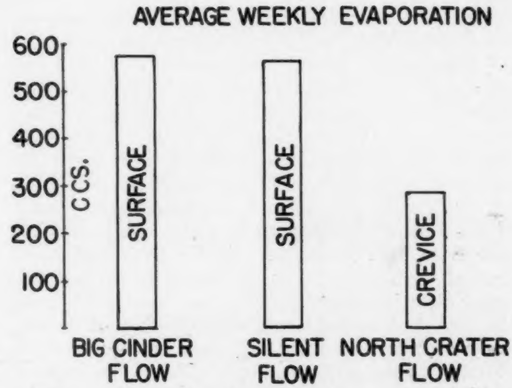

FIG. 9. Evaporation for the period Aug. 6-27, 1938; North Crater Flow—10 inches below the surface; Big Cinder Butte and Silent Flows—17 inches above the surface.

While temperature and evaporation rates are to some extent a measure of the same factor, evaporation is more inclusive in that it shows also the effects of wind and humidity. Judging from these evaporation measurements plants in deep crevices would transpire less rapidly than more exposed plants. Soil too must dry less quickly.

VEGETATION CHARACTER AND SEASONAL LENGTH OF PHOTOSYNTHETIC PERIOD

While it has been possible to obtain some quantitative idea of temperature and evaporation conditions above the rock surface, edaphic influences have largely gone unstudied in this kind of habitat. In view of the impossibility of obtaining adequate instrumental data on subterranean water relations, the ecological character and growth habits of the vegetation itself were studied in the hope of gaining at least some indirect information concerning moisture conditions about the roots. To that end the following facts were compiled for the more important flow species: (a) how much of the summer season each has green leaves, (b) general facts regarding character of leaves—whether thick or thin, large or small—features associated with the terms xerophyte and mesophyte, and (c) the distribution and general habitat preferences of the species as reported in the various available "floras" dealing with this general region. Observations concerning seasonal activities were made at approximately weekly intervals during the period June 20 to September 15, in 1937 and 1938.

Conditions of growth, especially in relation to moisture, were interpreted from these data as far as was possible. The order of presentation parallels that to be used in the section on succession, starting with the rock surface habitat.

Plants of Bare Flow-surface Habitat. The xeric nature of the lava surface is attested by the character of plants which grow there, only crustose and foliose lichens being found. It is only after soil has been added that vascular plants succeed in becoming established.

Plants of Joint Habitat. Only two plant species, *Aplopappus nanus* and *Chrysopsis hispida*, have been found growing in joints. Both grow with their stems fully exposed and without protection against sun and wind; their roots penetrate into narrow joints in the rock, being so tightly wedged that it has not yet been possible to excavate a root system from a flow. No information has been obtained regarding the depth of root system nor soil and water conditions extant in the joints. Aplopappus is a low shrub, growing here from 6 to 18 inches tall; the roots and basal part of the stems of Chrysopsis are woody but the upper stem is herbaceous. Neither species has been observed to lose its leaves during the period over which observations were made, and they appeared to be carrying on photosynthesis. The leaves have a xeric appearance.

Plants of Shallow Crevice Habitat. None of the shallow crevice species is green and active over the entire summer; many cease activity early in July, all but *Pentstemon deustus* by August 10. A few plants of that species have been observed with a small number of green basal leaves until the end of August.

With one exception, all of the more important species are said to grow elsewhere at elevations corresponding to their location in the Monument. The exception is *Drymocallis pseudorupestris*, the most abundant species in shallow crevices, which definitely has the appearance of a mesophyte. It is reported to grow from the submontane to the subalpine zones (Rydberg, 1917). Another interesting but rather rare species here is *Erigeron trifidus*, which is an alpine plant (Tidestrom, 1925; Rydberg, 1917).

There is no significant correlation, here, between altitudinal distribution, leaf character, and drought resistance. Apparently there is ample water for all species, both mesic and xeric, during spring and early summer; in middle and late summer there is no available water for any of them.

Plants of Deep Crevice Habitat. Two deep crevice species, *Chamaebatiaria millefolium* and *Sericotheca glabrescens*, have green leaves throughout the season of observation. *Woodsia scopulina* had largely ceased vegetative activity before June 20, *Brickellia grandiflora* var. *minor* by the end of July; *Philadelphus Lewisii*, varying somewhat with individuals, stopped activity and lost most of its leaves between July 10 and August 10. *Dryopteris Filix-mas* grows until cold weather comes; some have been observed late in September, still very green.

Most of these species are normally found at higher elevations, where moisture is a less critical factor than in the region of the Monument. Sericotheca is reported to grow in the piñon and yellow pine belts; Philadelphus, Brickellia, Woodsia, and Dryopteris in the submontane and montane (Abrams, 1923; Rydberg, 1917; Tidestrom, 1925). Only Chamaebatiaria is reported for the Artemisia belt. It grows also at higher elevations (Tidestrom, 1925).

Judging by usual distribution and ability to continue growth throughout summer, Chamaebatiaria and Sericotheca are the most drought resistant of the deep crevice plants. The distribution and general character of the other four species would lead one to call them mesophytes, and it is surprising to find such an ecological type represented in a region so definitely xeric. Their presence in the deep crevices indicates that moisture conditions are favorable, and this corroborates the evidence obtained from temperature and evaporation measurements.

Plants of Old Soil-covered Flow Habitat. A greater number of individuals on old flows and character of the dominant species indicate that an accumulation of soil has materially improved moisture conditions. It may be possible that there is more water, at least early in the season, in deep crevices; but the more uniform distribution of vegetation and the fact that a majority of its dominant shrubs are green all summer suggest that water is available for a longer time and in greater total amount on the old flows.

Three shrubs whose leaves have been seen to keep their greenness until September 15 are *Artemisia tridentata, Purshia tridentata, Chrysothamnus nauseosus*, and *Eriogonum microthecum*. Two other dominant shrubs, *Leptodactylon pungens* and *Eriogonum heracleoides*, cease vegetative activity early in August.

Floristically, an old flow community is composed of species which grow in the Artemisia belt. All of the important herbs, and five of the six first-ranking shrubs are so reported (Rydberg, 1917; Tidestrom, 1925). The only exception is *Eriogonum heracleoides*, which is reported for the submontane and montane zones.

SUCCESSION ON PAHOEHOE FLOWS

FLOW AGE CORRELATED WITH SPECIES NUMBER AND SPECIES DENSITY

Vegetation succession was studied by selecting pahoehoe flows of various ages, upon which quadrats were laid out. Tabulations of all vascular plants found within the plots were made. This work was done late in June, 1938, when both spring ephemerals and summer flowering plants were visible.

The only published geologic work on the Monument is that of Stearns (1930) and his conclusions regarding age of the lava have been largely followed in this work. He tabulated 27 of the lava flows in order of "approximate eruptive sequence." Six representative flows, including what he believes to be the oldest and the youngest, were selected for these successional studies. The quadrats were laid out as follows: flows are listed in order of increasing age: 1. Indian Tunnel Flow, 10 10-by-10 meter plots (Station 11 of Fig. 6); 2. North Crater Flow, 10 10-by-10 meter plots (Station 7 of Fig. 6); 3. Northwest Big Craters Flow, six 10-by-10 meter plots (Station 4

of Fig. 6); 4. Flow between Half Cone and Crescent Butte, 10 five-by-five meter plots (Station 6 of Fig. 6); 5. Northeast Flow from Big Cinder Butte, 10 five-by-five meter plots (Station 5 of Fig. 6); 6. Silent Cone Flow, five five-by-five meter plots (Station 3 of Fig. 6).

To eliminate personal bias in selecting the locations for the plots, they were arbitrarily spaced a predetermined distance apart, in most cases 20 meters from center to center. The greater uniformity of vegetation on older flows warrants the use of smaller and fewer quadrats there.

To facilitate comparison between the various flows, the densities are expressed uniformly on a basis of 1,000 square meters for each (Table 4). (Density as used here refers to the number of individuals of a species per 1,000 square meters of surface area.)

The total of 52 species of vascular plants occurring in the quadrats fall quite naturally into three groups: (1) those which increase for a time and then decrease as flow age increases, pioneers in general (Table 4*a*); (2) those which become increasingly important as flow age increases and attain their greatest density on the oldest flows, climax species (Table 4*b*); and (3) a group composed of species which follow no definite sequence or are too limited in number to give any indication of successional trends (Table 4*c*).

The youngest flow, having had the least time to progress from a sterile condition, has the smallest number of species, 12, and the lowest total density, 269 individuals per 1,000 square meters. On the other flows, which together represent an age span of several thousands of years, the number of species increases with flow age. There is also a substantial increase in total number of individuals with age increase; the oldest flow has 28 times as many as the youngest.

TABLE 4. Densities of lava flow species per 1,000 square meters on each flow.

	Indian Tunnel Flow	North Crater Flow	N. W. Big Craters Flow	Flow between Half Cone and Crescent Butte	N. E. Flow from Big Cinder Butte	Silent Cone Flow
4*a*—Species whose densities increase and then decrease with greater flow age.						
Trees						
Pinus flexilis	–	–	–	4	4	–
Shrubs						
Aplopappus nanus	–	13	102	108	120	–
Chamaebatiaria millefolium	1	61	89	32	24	–
Pentstemon deustus	47	320	114	500	472	128
Philadelphus Lewisii	5	72	130	–	–	–
Sericotheca glabrescens	–	20	–	32	4	–
Flowering herbs, except grasses						
Brickellia grandiflora var. *minor*	–	12	13	–	–	–
Drymocallis pseudorupestris	181	1001	240	604	548	–
Erigeron trifidus	–	28	20	–	–	–
Pteryxia terebinthina var. *foeniculacea*	2	394	–	100	48	–
Stephanomeria myrioclada	12	15	28	40	60	–
Grasses						
Stipa occidentalis	–	1	17	368	224	120
Ferns						
Dryopteris Filix-mas	2	–	–	–	–	–
Woodsia scopulina	3	–	2	24	–	–
4*b*—Species whose densities increase with greater flow age.						
Shrubs						
Artemisia tridentata	–	–	27	396	324	896
Chrysothamnus nauseosus	1	1	3	4	20	64
Eriogonum heracleoides	–	–	2	260	8	792
Eriogonum microthecum	–	–	–	292	184	112
Leptodactylon pungens including var. *Hookeri*	–	76	–	224	300	232
Purshia tridentata	–	23	2	128	112	432
Flowering herbs, except grasses						
Eriogonum aridum	–	2	–	36	44	64
Eriogonum ovalifolium var. *celsum*	–	–	–	–	4	152
Gayophytum ramosissimum	–	–	–	–	–	928
Navarretia Breweri	–	–	–	–	–	240
Grasses						
Agropyron inerme	–	–	–	–	–	512
Agropyron Vaseyi	–	–	–	–	–	648
Poa secunda	–	1	23	220	132	1632
Sitanion hystrix	5	12	145	264	280	208
4*c*—Incidental species which exhibit no apparent successional trends.						
Shrubs						
Eriogonum effusum	–	–	66	–	76	–
Flowering herbs, except grasses						
Achillea lanulosa	–	–	2	–	–	–
Castilleja Vreelandii	–	–	–	12	–	–
Chaenactis Douglasii	–	–	–	–	56	24
Chrysopsis hispida	–	–	–	–	40	–
Cirsium Hookerianum	–	1	3	–	1	–
Cryptanthe flexuosa	–	–	–	36	216	64
Delphinium megacarpa	–	–	–	–	–	96
Eriogonum depressum	–	–	–	12	88	–
Eriogonum subalpinum	–	34	–	36	4	24
Lithospermum pilosum	–	–	–	–	–	8
Lomatium triternatum	–	–	–	–	–	32
Mentzelia albicaulis	–	–	–	–	20	–
Opuntia polyacantha	–	–	12	–	–	24
Oreocarya sericea	–	–	–	60	68	–
Pentstemon cyaneus	–	–	–	–	–	24
Phacelia leucophylla	5	–	–	–	72	–
Phoenicaulis Menziesii	5	–	30	–	–	–
Polygonum Douglasii	–	–	–	–	–	8
Senecio altus	–	–	–	–	–	96
Senecio canus	–	–	–	–	–	24
Senecio uintahensis	–	–	–	12	–	–
Grasses						
Bromus tectorum	–	–	–	–	–	8
Oryzopsis hymenoides	–	1	–	24	72	–
Total species sampled on each flow	12	19	21	24	28	28
Total individuals sampled on each flow	269	2088	1070	3824	3651	7600

PROCESS OF VEGETATIONAL DEVELOPMENT

Rock Surface Prisere. Succession upon bare rock has been worked out many times, but it has usually been done in regions less arid than that under consideration here. As has been noted elsewhere, a rock surface prisere beginning with crustose lichens on the lava, and a crevice prisere where herbs and shrubs are the pioneers is found. But, in contrast to these other places, the rock surface prisere is found to be relatively unimportant. Fruticose lichens never come in and the smaller forms function mainly as aids in weathering. They do not grow densely enough to form a substratum for vascular plants. The crevice priseres are the most important.

Joint Prisere. The two species associated with joints, *Aplopappus nanus* and *Chrysopsis hispida*, persist a long time but their habitat is finally eliminated and they are succeeded by members of the climax community.

Shallow Crevice Prisere. The plants of shallow crevices are small and for the most part herbaceous; only one species is woody. The predominant species is *Drymocallis pseudorupestris* (Fig. 7). It has the highest density and occurs on all but the oldest flow. The species with the second highest density is *Pentstemon deustus*. It has woody roots and about 2 to 4 inches of woody perennial stem. Following these two, in approximate order of importance, come

Pteryxia terebinthina var. *foeniculacea, Stipa occidentalis, Stephanomeria myrioclada,* and *Erigeron trifidus.* There is less confinement of these species to a restricted habitat than is true of deep crevice species. Drymocallis grows exclusively in shallow crevices on flows, but the other species grow also on cinder cones.

Some difficulties were encountered in compiling density values for Leptodactylon because it was not realized while the field work was being done that certain variations in the group were constant enough to warrant a separation of the material into a species and a variety of that species. Further consideration has shown that there are two forms growing on the lava. The plants on old soil-covered flows, such as Silent, are largely *L. pungens. L. pungens* var. *Hookeri* is a shallow crevice plant, and all on North Crater Flow are probably of that variety. It is believed that both the species and its variety are found on flows intermediate in age, but because this was not recognized in the field there has been no separation in the density tabulations (Table 4*b*).

Several other shallow crevice plants were found in the plots on the flows, but only in small numbers. Two of these, *Achillea lanulosa* and *Castilleja Vreelandii,* grow more abundantly in the mountains north of the Monument, and the disseminules probably come from there. Three other incidental species have been observed only on young flows, *Cirsium Hookerianum, Phoenicaulis Menziesii,* and *Senecio uintahensis.* Other species more commonly associated with cinder cones occur on the flow in small numbers, and include *Eriogonum depressum, Mentzelia albicaulis, Oreocarya sericea,* and *Phacelia leucophylla.* One grass, *Oryzopsis hymenoides,* comes into this category also.

The roots of shallow crevice plants probably contribute humus to the soil, but it is likely that most of the above-ground parts blow away and lodge in deep crevices. In some places considerable amounts of vegetation are carried into crevices by conies (*Ochotona* sp.), which store them for winter food.

Exposure to winds retards the accumulation of soil in shallow crevices, so they persist as long or longer than near-by deep crevices. It is not uncommon to find parts of old flows bearing some pioneer stages of both bare rock and shallow crevice types that must have been maintained in that primitive condition for hundreds of years. Under such circumstances exposed lava surfaces with lichens, a shallow crevice with characteristic vegetation, and a deep crevice filled with soil and supporting a few Purshia shrubs of the climax vegetation, may all be found within a radius of a few feet (Fig. 10).

FIG. 10. North Crater Flow, showing vegetation in three habitats; rock surface at the right, shallow crevice in the center, and a nearly filled deep crevice at the left. July 16, 1938.

Deep Crevice Prisere. Seven species are characteristic of deep crevices; five of them here grow exclusively in such situations. Two of the five are shrubs: *Philadelphus Lewisii* and *Sericotheca glabrescens;* the other three are herbs: *Brickellia grandiflora* var. *minor,* and two ferns—*Woodsia scopulina* and *Dryopteris Felix-mas. Chamaebatiaria millefolium,* a shrub, is found in deep crevices but attains its best development on cinder cones. The seventh species, limber pine, occurs sparingly on pahoehoe flows (Fig. 11).

FIG. 11. Big Cinder Butte Flow, with scattered, dwarfed limber pines. In the distance is the Devil's Orchard where trees are larger and more abundant. June 21, 1938.

Individuals soon outgrow the crevices in which the seedlings start, and most of the tree is then exposed above the flow surface. Such pines are generally dwarfed and contorted and do not appear thrifty; reproduction is scanty.

The three shrubs, Philadelphus, Chamaebatiaria, and Sericotheca, are dominant in the deep crevice community; they supply the largest individuals and have the greatest density.

Deep crevice plants react upon their environment by supplying organic material which, in part at least, turns to humus. Considerable quantities of dead stems and leaves have been seen in the crevices, and it is likely that even in this dry climate much of it undergoes humification. The humus, along with the residual soil from flow weathering and the wind-transported soil, tend as time goes on to fill the crevices. In that way these species contribute to their own destruction, for when the crevices are filled, the physical protection that is afforded against the desiccating influence of wind and insolation ceases to exist and they are succeeded by the apparently more drought resistant climax species (Fig. 12).

Convergence of Priseres to Climatic Climax. All successions lead directly to the grass-sage climax as

rapidly as soil accumulates to a depth sufficient to support its deep-rooted members. Deep crevices are filled first, accompanied by a disappearance of their characteristic vegetation, while shallow crevices still

FIG. 12. Big Crater Flow at the left, Silent Cone Flow at the right. There is close correlation between amount of vegetation and age of flow. June 21, 1938.

persist. Eventually minor depressions are filled also and shallow crevice plants disappear. Coverage of intervening surfaces is aided by shrubs in the crevices; these impede wind movement sufficiently to cause deposition of aeolian material. Thus these flat flow areas that formerly maintained nothing higher than foliose lichens gradually come to support the regional climax (Fig. 13).

FIG. 13. Silent Cone Flow with vegetation which is probably the regional climatic climax type. June 20, 1938.

This final stage is dominated by six shrubs: *Artemisia tridentata, Purshia tridentata, Eriogonum microthecum, E. heracleoides, Chrysothamnus nauseous,* and *Leptodactylon pungens.* A less important shrub is *Eriogonum aridum;* another is *E. effusum,* which is very similar to *E. microthecum* in habit and close to it taxonomically. Just as typical of this community as the shrubs are certain herbs which occupy spaces between them. Five grasses are important: first is *Poa secunda,* then in order are *Agropyron Vaseyi, A. inerme, Sitanion hystrix,* and *Stipa occidentalis. Gayophytum ramosissimum* and *Navarretia Breweri* are the most important dicotyledonous herbs.

There are numerous herbaceous species which. here, attain their best development and greatest abundance on cinder cones, but which are also present on old lava flows. They appear to be a regular part of the climax vegetation. This group includes: *Chaenactis Douglasii, Cryptanthe flexuosa, Delphinium megacarpa, Eriogonum ovalifolium* var. *celsum, E. subalpinum, Lithospermum pilosum, Pentstemon cyaneus,* and *Polygonum Douglasii.* Three other herbs, *Lomatium triternatum, Senecio altus,* and *S. canus,* have been seen only on old flows. Prickly pear, *Opuntia polyacantha,* grows on old flows and also on old cinder cones.

Old flows in this area, like all accessible grass-supporting flows on the Snake River plains, have been grazed to some extent, but probably less than is usual; the disturbance thus produced may be responsible for the introduction of certain weedy plants, such as *Bromus tectorum* (Table 4c).

AA LAVA FLOWS AND THEIR VEGETATION

RATES OF SUCCESSION ON PAHOEHOE AND AA LAVA FLOWS

Succession on the aa type of lava flow has not been studied statistically in the Monument. A general survey indicates that pahoehoe flows tend to become completely covered with the grass-sage climax before aa flows of like age. A specific instance is a flow about 5 miles east of Carey which contained both lava types. The pahoehoe portion supported the typical grass-sage community members; the aa had some of these species in places, but more of its vegetation was characteristic of earlier successional stages. Chamaebatiaria and Sericotheca were there, growing between blocks of lava, suggesting that conditions were similar to those of deep crevices on smooth flows. Much of the aa flow remained void of soil and hence it bore less vegetation than the pahoehoe.

The greater advance of vegetation on pahoehoe is evidently due to the fact that less soil is required to cover this nearly smooth and level kind than an aa flow with its great surface irregularity. Surfaces of some aa flows are serrate in profile and the ridges may be bare of vegetation and soil while low areas between, where soil has accumulated, support a good growth. As a major part of the soil mantle that accumulates on the flows is transported, the time required to complete the process would be proportional to the amount of soil required.

Elsewhere, in regions of greater precipitation and where more residual soil accumulates, conditions may well be quite different. Stearns (in correspondence) reports that he has observed flows in Hawaii and also in Oregon where aa has a dense vegetation covering, while equal-aged pahoehoe is still quite bare. He believes the subject of succession rate on pahoehoe and aa is "too variable to be covered in any general statement." Nevertheless, it seems worth while to report conditions as they are in individual cases. From many such it may be possible eventually to generalize.

Relation of Limber Pine Distribution to Flow Physiography

DISTRIBUTION ON PAHOEHOE FLOWS

Limber pine is sparingly present on certain pahoehoe flows, including Big Cinder Butte Flow, and the flow between Half Cone and Crescent Butte. On others, such as Indian Tunnel Flow, only a very few pines are found; on still others, as Silent Cone Flow, there are none (Fig. 13). This is shown by the density studies as given in Table 4.

No obvious reason for the erratic distribution of pine on flows presented itself, but it was thought successful establishment might be correlated with protection by cinder cones against drying winds. This assumption was reached because Big Craters Flow with few trees and Silent Cone Flow with none lie to the west (to windward) of the line of cinder cones; the two flows having fair tree growth lie in the lee of the cones (Fig. 6). To test this theory evaporation measurements were made. Livingston white sphere atmometers were placed on Silent Cone Flow and on Big Cinder Butte Flow, a pair on each (Stations 5 and 3, Fig. 6). Records were kept for four weeks in July, 1938. Evaporation rates at the two sites were almost identical for the period, as is recorded by the first two units of the histogram (Fig. 9). Thus the manner of distribution of pine does not seem to be due to a difference in evaporation.

DISTRIBUTION ON AA FLOWS

Further investigation throughout the Monument and adjacent region revealed that the best pine stands on lava—those with the largest trees, the most individuals, and having the best reproduction—are mainly in two areas, as bounded within the black lines of Figure 6. One area extends northeast from Inferno and Paisley Cones and includes the area popularly known as the Devil's Orchard; the other lies west (to windward) of the line of cinder cones, starting at approximately the south end of Big Cinder Butte, and extending in a south and easterly direction to the end of the Monument, paralleling the lines of cinder cones. The presence of this area of pines to the west (windward) of the zone of cones further shows that the establishment of trees has no relation to the position of cones.

Both regions of best pine growth consist almost entirely of extremely rough aa flows. Most of the larger one to the south may be described by the term "sawtooth." Here are long, nearly parallel ridges with depressions 6 to 20 feet deep in between. Soil and snow collect in these depressions, and it is here that vegetation is found. Monoliths or fragments of old crater walls frequently protrude through the flows, and these further add to the topographic irregularities (Fig. 4).

Because the best development of trees on flows is associated with extreme surface irregularity, it was logical to look for a causal relationship. A reasonable explanation is that these flows offer the conditions necessary to the success of seedlings, namely, a reduction in evaporation intensity and an increase in soil moisture. It was not possible to make measurements of evaporation on these flows, but it may be expected that it would be reduced in depressions several feet below the general surface, or in the shade and protection of a crag 6 to 30 feet high. Monoliths frequently are of the latter height.

The probable benefits received by seedlings from even small increases in soil water can be seen in the results of a tabulation of the positions of 125 trees, exclusive of seedlings, selected at random on Derelict Flow, a large aa flow in the southern tree area. Trees grow here in depressions where snow would accumulate in considerable quantity in winter; in addition it was found that in a majority of cases they grow where run-off from exposed rocks would collect. Seventy-eight of the trees were growing at edges of rock outcrops; 14 others grew within 4 feet of such outcrops. Only 33 were more than 4 feet away.

It is thus evident that trees occupy positions on aa flows where water collects and where evaporation is reduced, and it is probably the case on pahoehoe also. Pine on pahoehoe is a typical deep crevice plant; its seedlings apparently must start in protected sites in order to succeed. When deep crevices which afford these conditions disappear, pines, like other deep crevice plants, also disappear, and the grass-shrub regional climax is finally attained. This is well illustrated on Silent Cone Flow.

The problem of why there are almost no trees on certain young flows, as Indian Tunnel Flow and Big Craters Flow, is still unanswered. A possible explanation is that the flows are too young and there has been insufficient time for them to become established.

CINDER CONES AND THEIR VEGETATION

Growth Conditions on Cones

GENERAL FEATURES

In contrast to flows, which are nearly level, there appear on cinder cones the indirect effects of topography, which, in this semiarid region, are responsible for rather marked differences in the character of vegetation on north- and south-facing slopes. Another difference between flow and cinder cone vegetation is due to the physical character of the lava itself. Vascular plants do not grow on flows until soil accumulates; then they are limited to crevices for a long time. The very youngest cinder cones support vascular plants quite generally, and there is no reason to believe that any change in cinders was necessary before these plants could start.

Three community types include essentially all vegetation to be found on the cones. A pioneer community of herbs occupies a major part of young cones (Fig. 14); it decreases in proportion of area covered as cones become older, until finally it is restricted to only the most exposed parts of southwest slopes. A second community, in which trees are dominant, is confined to protected sites, chiefly on north-facing slopes (Fig. 15); it occasionally is found in

depressions on south slopes also. The third type is dominated by shrubs and occupies south slopes of old cones; it may be entirely absent from young cones (Fig. 16).

FIG. 14. South side of North Crater. Alternating light and dark zones indicate low, wind-formed ridges. Small white spots are *Eriogonum depressum;* in the foreground they grow in old wagon tracks. July 20, 1938.

FIG. 15. North side of North Crater. Depressions support trees while ridges have only herbs. July 16, 1938.

FIG. 16. Shrub community on southwest side of Silent Cone. July 19, 1938.

HABITATS OF CONES AND HOW THEY CHANGE AS CONE AGE INCREASES

Growth conditions on young cones are modified slowly, and then only as a result of change in soil and in micro-climatic influences brought about by the vegetation which succeeds in getting started. Without vascular plants of sufficient size to serve as windbreaks weathered material does not remain in place, but blows away, and even after some hundreds of years cinders at the surface of little vegetated parts of cones are unweathered. Vegetation also adds humus, resulting in a greater ability of soil to supply water to plant roots. Such superior

FIG. 17. Road cut with plants growing in a narrow seam of weathered soil; unweathered cinders above and below support little vegetation. July 8, 1938.

water-supplying ability of fine-textured soil over that of unweathered cinders was demonstrated in a striking manner in a road-cut in the Monument, near Station 7 (Fig. 6). A seam of weathered material about 3 inches thick lay between unweathered cinders, below and above. As can be seen in Figure 17, plants are nearly absent from the cut except in the narrow seam of fine soil, where many are found. Finer texture evidently gives this soil better moisture conditions than are present in the coarser, unweathered cinders adjoining.

Accompanying the change in soil texture is one in color, which goes from black to gray or light brown, as weathering products accumulate. The effect of this alteration is to reduce light absorption, and thus soil temperature on bright summer days.

CINDER CONE SOILS

Unweathered cinders are coarse, some being as much as 3 to 4 inches in diameter, but the average is about one-fourth inch. There is usually more or less interstitial material of sand size mixed throughout. Cinders are usually light in weight, porous, and are sometimes soft enough to be crushed between the fingers.

Although large areas on cinder cones have remained devoid of vegetation, except for small herbaceous species which are not very effective as soil-binders, there has been little mass movement of cinders. No deposit approaching the size of dunes is found. The surface in some herb communities is rippled, but these ripples are only 4 to 6 inches in height (Fig. 14).

FATE OF PRECIPITATION

Here, as on the flows, there is little or no surface run-off. There flatness of surface and frequency of crevices is responsible, but on the cones it is due to porosity of cinders. Water usually sinks in immediately. Rarely, during extremely violent rains, rivulets flow for 100 or 200 feet before disappearing.

Absence of water loss would be expected to result in conservation of much of it for use by vegetation. But the same property which gives a cinder soil almost limitless ability to absorb water probably permits much of it to sink deeply, beyond the reach of plant roots.

Prevailing southwest winds cause winter snows to be concentrated on northeast sides of cones at the expense of the supply on southwest sides. Because of its protected position and greater initial quantity this snow persists, and furnishes moisture to vegetation after that on exposed southwest slopes has melted. This is strikingly shown by a photograph taken on April 3, 1939, by Helen K. Sharsmith (Fig. 18) which also illustrates the close correlation between position of snow and vegetation.

FIG. 18. Snow persisting on northeast sides of cones when southwest sides are bare; positions of snow and vegetation coincide. Spatter cones in foreground; Half Cone and Crescent Butte, left distance; Broken Top, center; Big Cinder Butte, right. Photograph by Helen K. Sharsmith. April 3, 1939.

SOIL MOISTURE

Water-retaining Ability of Cinder Soil. Water relations of unweathered cinders cannot be compared with those of gravel or other soils of comparable particle size. Water is not confined to the outer surfaces of cinders, but penetrates within as well; thus water-retaining ability is higher than might be expected.

Measurements were made of water-retaining capacity of unweathered cinders of three different textures; also, for comparison, of a fine-textured soil from an old lava flow. Two of the cinder samples were prepared by combining 25 lots of unweathered cinders. This mixture was separated into two lots with a 2 mm. soil sieve. A third lot consisted of coarse, unweathered, unassorted cinder soil collected from North Crater (Fig. 19). Sample 4 was aeolian material from an old flow. A 500 cc. soil tube, 26.5 centimeters tall, was filled with soil from each sample. Each lot was kept wet for three days, excess water was then drained until presumably there was no gravitational water left. Water content was determined for each sample both as a percentage of its dry weight and of its volume. The values are recorded in Table 5.

TABLE 5. Water-retaining ability of four soils.

Sample	Soil type	Water as percentage of weight	As percentage of volume
1	Cinder material over 2 mm.	74.7	23.7
2	" " 2 mm. and less	73.8	53.2
3	" " fresh, unassorted	89.6	26.2
4	Old flow surface soil (aeolian)	41.7	48.1

If calculated on a dry weight basis, the three cinder soils appear to have unusually high water-retaining capacities—values such as are associated with soils containing a considerable amount of colloidal matter. These values are excessively high because of the light weight of cinders; many have a specific gravity of less than unity. The coarser the soils, the greater is the difference between percentages of water computed according to the two methods. Sample 3 is probably the most porous in texture and its water content, in relation to its weight, is about 3½ times as great as that in relation to volume. For the clay and silt soils—sample 4—the values approach equality. For cinder cone soils in general it is probable that the water content in relation to weight runs about two to three times that in relation to volume.

Braun-Blanquet (1932) and Livingston and Koketsu (1920) state that the water-supplying power of a soil is much more closely correlated with water content expressed on a basis of volume than on a basis of dry weight. The present work certainly tends to substantiate those reports.

FIG. 19. Northeast side of North Crater. Soil sample site 1 was in the woods at the right, 2 at the upper end of the herb community in the foreground. Pine seedlings were studied in this herb community. White spots are *Eriogonum depressum*. July 16, 1938.

Available Water. Soil of a south-facing slope, receiving greater insolation and being more exposed to the prevailing southwest winds, might be expected to have a lower water content than a protected north-facing slope. To test this, and also to learn the depths to which roots must penetrate to find available water, moisture content and wilting coefficient values were determined at six stations. These were located as follows: site 1, wooded northeast base of North Crater (Fig. 19); site 2, herb community, middle of northeast side of North Crater (Fig. 19); site 3, herb community, middle southwest side of

TABLE 6. Available water.

	Depth in inches	1937 VALUES				1938 VALUES			
		June 29	July 15	July 29	Aug. 13	July 3	July 13	July 21	Aug. 1
SITE 1									
Pine woods,	3	.....	.....	.....	.....	0.00	9.30	0.00	0.00
northeast side	6	0.12	0.00	0.00	.....	10.73	15.75	2.51	0.00
of North	18	6.98	4.51	0.36	.....	16.97	15.57	1.49	6.30
Crater	36	17.76	16.07	14.58	.....				
SITE 2									
Herb com-	3	.....	.....	.....	.....	0.00	4.98	0.00	0.00
munity, north-	6	29.55	20.65	20.63	.....	34.73	23.92	10.90	24.49
east side of	18	61.32	68.88	60.74	51.63	54.84	62.48	58.99	52.32
North Crater	36	75.80	65.58	72.59	64.29				
SITE 3									
Herb com-	3	.....	.....	.....	.....	0.00	18.68	0.00	0.00
munity, south-	6	24.59	9.78	0.00	0.00	13.43	34.00	28.23	22.07
west side of	18	42.80	38.90	33.51	41.18	34.14	53.92	40.90	57.38
North Crater	36	41.93	40.02	46.13	40.91				
SITE 4									
Pine woods,	3	.....	.....	.....	.....	24.92	.....	0.00	.....
north side of	6	7.04	0.00	0.00	0.00	15.92	.....	18.25	.....
Silent Cone	18	21.32	31.17	13.99	23.72	24.92	.....	22.27	.....
	36	23.41	26.38	24.38	13.21				
SITE 5									
Pine woods,	3	.....	.....	.....	.....	0.00	.....	7.70	.....
north side of	6	12.62	24.45	9.86	.....	12.36	.....	12.12	.....
Silent Cone	18	30.16	32.04	28.68	.....	15.76	.....	11.73	.....
	36	32.56	35.45	36.50	.....				
SITE 6									
Herb com-	3	.....	.....	.....	.....	18.89	.....	3.77	.....
munity, south	6	23.74	0.00	0.00	.....	21.62	.....	25.07	.....
side of Silent	18	34.54	36.28	37.41	.....	28.53	.....	25.17	.....
Cone	36	29.35	31.74	28.79	.....				

North Crater (Fig. 20); site 4, pine woods near base of Silent Cone; site 5, middle of north side of Silent Cone, also pine wood; site 6, herb community on southwest side of Silent.

FIG. 20. Southwest side of North Crater. July 19, 1938.

At intervals of about 2 weeks, in 1937, soil samples were collected at depths of 6 inches, 18 inches, and 36 inches, and in 1938 at 3 inches, 6 inches, and 18 inches. After determination of water content each sample was divided into two parts, and moisture equivalent of each determined. These two values were averaged and wilting coefficient calculated. Available water is the difference between water present and wilting coefficient of a soil.

A usual procedure in determining soil constants is to consider only the portion below 2 mm. diameter, assuming water relations of the larger particles to be unimportant. Because of the nature of cinder material no separation was made here, and anything that would go into a soil centrifuge cup was included.

Measurements of available water, computed on a gravimetric basis, are given in Table 6. While these values are, as suggested earlier, not as accurate as if computed on a volumetric basis they do show where water is available and indicate relative amounts.

Rather surprisingly there were no outstanding differences in amounts of available water between north and south sides of cones and between herb and tree communities. Sites 1, 4, and 5 in pine woods have little more available water than sites 2, 3, and 6 in communities of small scattered herbs. Very likely there would be conspicuous differences earlier in the season.

These data show that upper layers may be deficient in available water by midsummer; five of the six sites had none at the 3-inch depth during at least part of the summer of 1938. At 6 inches, four sites lacked water in 1937 and one the next year. At no time during the sampling period was water entirely absent at 18 inches, but there was under 1 percent at site 1 in 1937. At one sampling, following a rain, there was nearly 30 percent of water at site 3 at a depth of 3 inches. In 9 days time this fell to under 6 percent—less than the wilting coefficient value, and 7 days later there was essentially no water. Roots of slow-growing plants probably would not elongate rapidly enough to keep ahead of the lowering zone of available water.

Plants on cones make sufficiently close contact with cinders to enable them to utilize water from the internal as well as from the external surfaces. Examination of root systems of many plants reveals that they quite commonly grow directly through the individual cinders. This has been a major handicap in excavating roots for careful study; it has been almost impossible to prevent breakage when separating them from cinders. Figure 21 shows a specimen of *Galium Watsoni* from North Crater, with cinders through which its roots have passed.

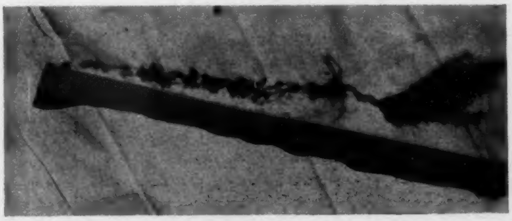

FIG. 21. Roots of *Galium Watsoni* passing through cinders. June 30, 1937.

SOIL TEMPERATURE

To find the magnitude of daily temperature fluctuations and to compare the rate of change of soil temperature with that of the air above, an air-soil thermograph was placed on a southern exposure of

a cinder cone, in an area as free of vegetation as could be found. In the soil, measurements were begun at a 3-inch depth, and this was increased 3 inches each week, records being taken during the latter half of June and during all of July, in 1938. Air temperatures were taken in the shade, 3 inches above the soil surface, during the same period. As might be expected, surface layers of black, unweathered cinders heated readily when the sun was shining. At all hours of day and night temperature at a depth of 3 inches usually equalled or exceeded air temperature. The daily maxima, for a period of 10 days, ranged from 8° F. more than those of the air to 3° F. less; the average soil maximum was 2.6° F. higher than the air. The absolute maximum at a 3-inch depth was 94° F. These measurements were made in June; had they been made later in the season and at depths less than 3 inches, it is probable that much higher temperatures would have been recorded. At greater depths, 6 inches and over, temperatures were less extreme than those of the air.

Only a short time was needed for changes in air temperature to be recorded in soil also. At 3 inches the maximum and minimum usually came not more than an hour later than in the air; often they practically coincided. A close relation was observed at all depths. Even at 3 feet the soil temperature began to rise in the morning only about an hour later than the air. The small daily increase took place in from 2 to 4 hours. Decrease was less rapid during the night. The record for the week when measurements were made at 30 inches is presented in Figure 22.

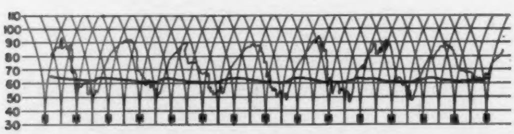

FIG. 22. Air and soil temperature records for the week of July 19-25, 1938, made on a cinder cone. Wide line is record at 30-inch depth; narrow line is shade temperature 3 inches above the cone surface. N = noon, M = midnight.

It apparently is rather unusual for soils to exhibit such rapid temperature changes at depths below the immediate surface. Weaver and Clements (1929) present records for a Nebraska prairie soil, taken at depths of 3 and 12 inches. The temperature trends and time of change at 3 inches followed the air quite closely, but those at a foot depth were several hours behind, the maximum being reached about midnight and the minimum shortly after midday.

It has been pointed out that in the region of this study daily air-temperature ranges are so great that shock may occur to the protoplasm of the aboveground parts of plants. Parts in upper soil layers are probably equally exposed to this danger, or even more so. High temperatures in this black soil may be fatal to tender plants, especially seedlings.

EVAPORATION

Direct effects of wind are not important in determining survival of plants upon cinder cones. There are a few contorted trees, and some breakage occurs, but a more important result is in increase in water loss—transpiration from plants and evaporation from soil.

Evaporation measurements were made for a period of 4 weeks in July, 1938, at three sites midway between the base and summit of North Crater. One site was on the southwest side of the cone in an area of herb vegetation (Fig. 20); one on the northeast side, also in an herb community (Fig. 19); the third was at the same elevation as the second, 175 feet from it, and about 25 feet within a pine woods. Atmometers were set up in pairs, the water reservoirs being buried sufficiently to bring the bulbs 10 inches above the cinder surface.

For the whole period evaporation in the herb community on the southwest side was 2,378.8 cc., on the northeast 1,989.5 cc., a ratio of about six to five. In the pine woods it was 1,477.9 cc. Reduced evaporation in the pine woods as compared to the near-by herb community can be attributed to the effect of vegetation, in providing shade and acting as a windbreak. The ratio of evaporation in the southwest herb community to that in the northeast pine woods is eight to five. The greater evaporation in the southwest is due to wind differences and to effects of increased saturation deficit, resulting from direct insolation. The effect of this is more rapid loss of water from the above-ground parts of plants and more rapid drying of soil surface layers.

VEGETATION CHARACTER AND SEASONAL LENGTH OF PHOTOSYNTHETIC PERIOD

A study of growth habits and ecologic character of important species found on cinder cones was made in a manner similar to that followed for the lava flows. The following facts were compiled: (a) time of year when each flowers, (b) time of year when fruits mature, (c) time it has green leaves, (d) ecologic character of leaves, (e) distributional preference of species as reported in various "floras," and, for many of the species, (f) studies on the nature of root systems and their vertical extent.

Plants of Herb Community. Members of the pioneer community are few in number of species and individuals, and small in size. Only a small part of the cinder surface is covered by plants. Five important species fall into three distinct groups, based primarily on differences in length of season of vegetative activity of leaves and depth of root systems; anatomical characters of leaves differ somewhat within groups, especially the third.

Eriogonum depressum, the most abundant species in the community (Figs. 14 and 19), is in a class by itself in that it is the only one which has green leaves throughout the summer. These have a xeric appearance; they are small, densely covered with white tomentum, and are crowded into a close cluster

near the ground; exclusive of the flower scape the plant is not over 2 inches tall. Its root system extends vertically downward with little branching. The longest one excavated went down 46½ inches; several others were nearly as long. It is interesting that seedlings as well as mature plants have deeply penetrating root systems. Seedlings have been observed which, in their first growing season, had roots a foot long by August. This may partly account for the success of this species. Its reported distribution is from the montane to the alpine zones.

A second group includes two species: *Chaenactis Douglasii* and *Phacelia leucophylla*. Both are taller than Eriogonum, being from 8 to 14 inches high. Both have green leaves, xeric in appearance, until about midsummer. Those of Chaenactis are finely cut and somewhat floccose; those of Phacelia are thick and densely canescent. The root systems are less deep than those of Eriogonum; those of Chaenactis being from 8 to 12 inches, and Phacelia's from 14 to 18 inches, in the individuals measured. Both species are here growing within the range of their usual distribution.

The third group includes *Mimulus nanus* and the bitterroot *(Lewisia rediviva)*. Mimulus is an annual, and most individuals have fruited and died by July 15, many before that time. It has small, thin leaves which have a definite mesic appearance. Its root system is shallow and usually does not extend downward over 4 inches. Lewisia is a perennial. A crown of more or less cylindrical fleshy leaves expands very early in the spring when soil moisture is plentiful. Late in June, as the large, delicate flowers mature, the leaves gradually wither and dry. By early July, when the fruits are ripe, above-ground parts are scarcely visible. Its roots are also fleshy and extend laterally several inches, but vertically only about four. Both Mimulus and Lewisia grow here within their general altitudinal range.

These three groups exhibit a direct relationship between length of activity period of the leaves and vertical extent of root system. One can well suppose there is also a relationship to available water. Activity of shallow-rooted Mimulus until the end of June indicates the presence of available water to within about four inches of the surface. Deeper-rooted Chaenactis and Phacelia find water somewhat longer at depths of 8 to 14 inches. Measurements of available water (Table 6) showed it to be present at such depths most of the summer and the plants probably have not exhausted the supply by the time they cease growth. *Eriogonum depressum* can find ample water all summer at the depths to which its roots penetrate.

There are indications in some places in this community that surface conditions may be as influential in determining plant density as moisture. A cinder surface from which the fine-textured material has been blown away is an inhospitable germination bed, but slight disturbance, such as is brought about by the walking of man or other animals, or by the wheels of vehicles, seems to improve it. The location of tracks may remain plainly marked for years by the perennials which become established in them (Fig. 14). It is not known whether the tracks merely cause a concentration of disseminules or whether they offer improved growing conditions. Soil may blow into the depressions, and it is probable that compacting of cinders improves water-retaining ability. In any event plants do grow more densely in these tracks than elsewhere and it shows that root competition may not be the critical factor which determines their wide spacing in the community.

Plants of Tree Community. The tree community, found mostly on north-facing slopes of cinder cones, is composed of three tree, and a small number of shrub and herb, species. Limber pine occurs on most cones, aspen *(Populus tremuloides)* and Douglas fir on a few old ones which have steep north slopes. The usual distribution of Douglas fir in zones from the submontane to the subalpine suggests that moisture conditions where it is found here are favorable. The similar distribution and mesophytic leaves of aspen further indicate this, as does successful maintenance of pine, when once it has become established.

Plants of Shrub Community. A consideration of herbs and shrubs in the tree community, and also in the shrub community of south slopes, yields little information on moisture conditions of their habitats. The species are less confined to a restricted habitat and most of the important ones are common to both of these communities; some are also in the climax community of old flows. Moisture conditions in the shrub community appear to be intermediate between those of the herb and tree communities.

SUCCESSION ON CINDER CONES

CONE AGE CORRELATED WITH SPECIES NUMBER AND SPECIES DENSITY

To demonstrate the changing character of vegetation with increasing cone age density studies were made of two communities on North Crater, a young cone, and of three on Silent Cone, an old one (Fig. 6). The herb communities were studied in meter-square plots. Six were spaced as equidistant as possible on two sides—northeast and southwest—of North Crater (Figs. 19 and 20), four others on the upper half of the south side of Silent Cone, the only part which supports the herb community type. For purposes of comparison densities have been computed on an areal basis of 6 square meters for each (Tables 7*a* and 7*b*).

The herb community on North Crater is composed of few species, only five being found in the plots; *Eriogonum depressum* has the highest density. In the community on older Silent Cone 10 species were found in the plots. *Eriogonum depressum* is absent, first place being taken over by Chaenactis. *Elymus condensatus*, a grass, has second place. The presence of seedlings of Purshia and sage suggests that shrubs are invading this last bit of herb community on Silent Cone and that it will, in time, be dominated by them.

Tree communities were studied near the northeast bases of the cones, where the densest growth occurs. On each cone eight 10 by 10 meter plots were spaced 15 meters from center to center; trees were tabulated in these and grouped in size classes as in Tables 7*c* and 7*d*. Shrubs were counted in 2 by 8 meter plots, one in a predetermined corner of each larger one (Tables 7*e* and 7*f*). Herbs were counted in 1 by 5 meter plots in the same corners (Tables 7*g* and 7*h*).

Older Silent Cone supports a denser tree growth than North Crater, there being 161 individuals to 53 in comparable areas. Douglas fir is present on Silent Cone and seems to prevent pine from attaining the size it does on North Crater, but there is little reproduction and this species probably will not become more important.

Both tree communities contain five shrubs, and in both Purshia is definitely dominant. The Silent Cone community has more herbs than the North Crater one, both in number of species and individuals. Gayophytum occupies first place in the latter while in the former *Agropyron inerme,* a grass, has that distinction.

North Crater has no shrub community while the south side of Silent Cone is almost covered by one (Fig. 16). Six 5 by 5 meter plots were laid out there for the study of shrubs; herbs were tabulated in a part of each (Tables 7*i* and 7*j*). Artemisia and Purshia are the dominant members. *Crepis acuminata, Mentzelia albicaulis,* and Gayophytum are important herbs. Four species of grasses occurred in the plots.

PROCESS OF VEGETATIONAL DEVELOPMENT

Herb Community. The herb community which covers a major part of young cinder cones is the earliest successional stage represented on them today. Judging by the present condition of the cinders, it is probable that it has existed almost since the formation of the cones.

Tree Community. On the north slopes the pioneers are being succeeded by a tree community, first in areas where moisture conditions are most favorable —in depressions and near the cone bases, then in adjoining parts having less protection. Pine and Purshia lead the way in the invasion. When these are established and moisture conditions improved other species join them.

To study the manner of limber pine migration and the degree of success of its seedlings, observations were made regularly during the summer of 1938 in an area on North Crater which is being invaded by pine. The plot was about 180 by 150 meters in size. It was bounded on three sides by pine woods and there were a few scattered trees on the fourth (Fig. 19); thus an ample seed supply was available. As the area lay near the northeast base of the cone moisture conditions were thought to be quite favorable. The positions of seedlings were mapped late in June and records of their vigor were kept periodically until August 18th.

A total of 105 seedlings were in the plot; seven grew singly, the rest in clumps of from two to eight. Most were within 25 meters of the seed trees; the farthest removed was 45 meters.

TABLE 7. Density values for species found in the communities on North Crater, a young cone, and Silent Cone, an old cone.

NORTH CRATER

7*a*. Herb community; six 1 meter plots.

Chaenactis Douglasii	6
Eriogonum depressum	22
Lewisia rediviva	2
Mimulus nanus	6
Stipa occidentalis	1

7*c*. Trees in tree community; eight 10 by 10 meter plots. Diam. at 4 feet.

Pinus flexilis	
Under 1 in.	12
1-3 in.	14
4-8 in.	19
9 in. plus	8

7*e*. Shrubs in tree community; eight 2 by 8 meter plots.

Artemisia tridentata	1
Chrysothamnus nauseosus	4
Pentstemon deustus	1
Purshia tridentata	127
Ribes cereum	7

7*g*. Herbs in tree community; eight 1 by 5 meter plots.

Eriogonum ovalifolium var. *celsum*	1
Eriogonum subalpinum	8
Gayophytum ramosissimum	74
Mimulus nanus	26
Phacelia leucophylla	4
Poa secunda	5
Sitanion hystrix	22
Stipa occidentalis	3

SILENT CONE

7*b*. Herb community; six 1 meter plots.

Artemisia tridentata	2
Bromus tectorum	2
Chaenactis Douglasii	20
Delphinium megacarpa	3
Elymus condensatus	14
Eriogonum vimineum	5
Mimulus nanus	3
Phacelia leucophylla	2
Pteryxia terebinthina var. *foeniculacea*	2
Purshia tridentata	6

7*d*. Trees in tree community; eight 10 by 10 meter plots. Diam. at 4 feet.

Pinus flexilis	
Under 1 in.	66
1-3 in.	64
4-8 in.	24
9 in. plus	0
Pseudotsuga taxifolia	
Under 1 in.	2
1-3 in.	0
4-8 in.	0
9 in. plus	5

7*f*. Shrubs in tree community; eight 2 by 8 meter plots.

Chrysothamnus nauseosus	11
Leptodactylon pungens	2
Pentstemon deustus	11
Purshia tridentata	101
Ribes cereum	30

7*h*. Herbs in tree community; eight 1 by 5 meter plots.

Agropyron inerme	136
Chaenactis Douglasii	21
Crepis acuminata	2
Cryptanthe flexuosa	3
Delphinium megacarpa	2
Drymocallis convallaria	5
Eriogonum depressum	2
Eriogonum subalpinum	5
Gayophytum ramosissimum	96
Mentzelia albicaulis	53
Mimulus nanus	11
Nicotiana attenuata	11
Phacelia leucophylla	22
Poa secunda	11
Polygonum Douglasii	19
Pteryxia terebinthina var. *foeniculacea*	3
Sitanion hystrix	21
Stipa occidentalis	2

7*i*. Shrubs in shrub community; six 5 by 5 meter plots.

Artemisia tridentata	85
Chrysothamnus nauseosus	3
Purshia tridentata	79
Ribes cereum	1

7*j*. Herbs in shrub community; six 1 by 5 meter plots.

Agropyron Vaseyi	2
Chaenactis Douglasii	2
Crepis acuminata	37
Delphinium megacarpa	2
Elymus condensatus	1
Eriogonum aridum	1
Eriogonum ovalifolium var. *celsum*	2
Eriogonum subalpinum	6
Gayophytum ramosissimum	30
Lithospermum pilosum	5
Mentzelia albicaulis	44
Mimulus nanus	2
Phacelia leucophylla	14
Poa secunda	9
Sitanion hystrix	14

On July 5th, 14 seedlings were alive; on the 16th, 10; on the 27th, four; on August 3rd, four; on August 18th, the last time observed, three.

It is evident that seeds were produced in ample quantity to reproduce the species, that they were well disseminated, that many germinated, but that few, if any, survived through the first summer. The high mortality rate may be due to their shallow root systems or to high temperatures in upper soil layers. Most of the root systems had a vertical length of only about 3 inches at the time the plants died; the longest excavated was $5\frac{1}{2}$ inches.

Occurrence of seedlings in clumps, never associated with pine cone remains, suggests that rodents are the agents of pine seed dissemination, and that the clumps mark the sites of seed caches. There are two species of chipmunks and three of ground squirrels in the Monument which might carry pine seeds. Their food habits lead the writer to think that ground squirrels are largely responsible. The one most commonly associated with the younger cinder cones is Hollister's Ground Squirrel, *Citellus lateralis tescorum*.[3] Limber pine seeds are wingless and wind dissemination would be unimportant but rodents spread them very well. An advantage of rodent dissemination is in the greater likelihood of germination when buried, but a disadvantage is introduced in that several seedlings together must compete for water.

The ground squirrel is an effective agent for Purshia dissemination also, clumps of seedlings being found almost as frequently as are pine. These often contain many individuals; 21 in one group were counted on North Crater. Competition for water in such situations must be very keen.

A measure of the rate of invasion of an herb community by pine was obtained by studying ages of trees near the edge of a southward advancing woods on the east side of Inferno Cone, one of the youngest in the Monument. A transect 25 meters wide was laid out in a north-south direction, extending inward 160 meters, from the southern margin of the forest. Ages of all trees an inch or more in diameter at a height of about 4 feet, were determined from increment borings. There were no large dead trees and it seems likely that the present living ones are the first to occupy the site.

The trees of the transect were found to be unevenaged, ranging from over 150 years down to 13 years. They are located in three quite compact and distinct groups, each composed of trees of varying ages. Between the three main bodies the herb community still persists, or there are numerous pine seedlings and small trees. The northernmost forms the southern margin of the nearly continuous pine forest; the other two are outposts beyond it. This suggests that the forest advance has not been unbroken and uniform, but that one or more trees became established at a distance from the seed source and that then others filled in about them. The southern tree island was apparently established before the center one, as it contains older trees.

The rate of invasion has been very slow. In more than 150 years the forest margin has advanced 37 meters; in over 121 years only 12 meters, and that only in the form of a single small tree under an inch in diameter. But this tree may be the nucleus for another island of trees.

Shrub Community. On south slopes the herb community is slowly succeeded by shrubs. Purshia is the pioneer in this invasion. It has an extensive root system and is able to withstand partial burial, by wind-borne cinders, to which isolated shrubs on cones are subject. Its branches apparently elongate sufficiently to keep above the surface, and they send out adventitious roots wherever contact is made with soil. Thus Purshia makes a very good surface stabilizer. Only after it has become sufficiently abundant to prevent further burial and has helped to bring about an accumulation of fine-textured surface material does sage become important in the community.

Convergence to Climatic Climax. As old cones are eroded away and approach flatness they come in time to support the regional climax type of vegetation. This is not now occurring in the Monument because cones of sufficient age are lacking, but it is evident in several instances in the vicinity of Big Butte (Fig. 1). Both the tree and shrub communities lead to the climax, the former by undergoing a complete loss of trees and an increase in grasses, and the latter through a reduction in shrubs and an increase in grasses.

SUMMARY

The Snake River plains of southern Idaho have been built up by many volcanic eruptions which have occurred over a long period of time, Miocene to Recent. Most of the volcanic material is in the form of lava flows, but cinder cones are common, especially in the area of the Craters of the Moon National Monument, in the north-central part of the plains. There some of the most recent volcanic activity has taken place, and cones and flows of various ages are present.

Primary succession on pahoehoe lava flows and upon cinder cones was studied within the Monument and in immediately adjacent areas. General observations were also made on the vegetation of aa flows. Consideration has been given to possible causes for the presence of trees on flows in certain restricted areas on the Snake River plains and their absence from others.

A young pahoehoe lava flow presents four distinct vegetation habitats. The most extensive of these is the xeric, bare flow surface, where lichens are pioneer plants. A second habitat, much more limited in area, is that in joints. Shallow crevices furnish a habitat with a thin soil deposit for vascular plants but there is no protection for aerial portions of plants. Deep crevices provide the best moisture con-

[3] The writer is indebted to Philip M. Blossom, Associate Curator of the Museum of Zoology, University of Michigan, for the taxonomy of the rodents and for information on their food habits in the Monument.

ditions to be found on young pahoehoe flows, and in them several mesic herbs and shrubs are pioneers. Soil, partly residual, but mostly aeolian in origin, slowly fills all crevices and then deposits as a mantle over the flow surface. First deep crevice plants are eliminated because of the changing habitat, then shallow crevice plants, and finally joint and rock surface plants. They are all replaced by a grass-sage type of community which is probably the climatic climax of the Snake River plains region.

The Monument is near the center of an area of about 750 square miles where trees—mostly limber pines—grow scatteringly upon the flows. The best tree growth is on the roughest flows, mainly of the aa type, and old flows which are completely soil covered generally have none. Rough flows probably supply conditions which tree seedlings need for successful establishment: concentration of precipitation in depressions, and protection against strong desiccating winds.

North-facing and south-facing slopes of cinder cones present conditions of growth which are quite different, mainly in the rate of evaporation. On south-facing slopes, and on ridges and prominences of north-facing ones, a community of herbs provides the pioneers. Its members are well adapted to growth in this xeric habitat, by either ceasing growth early in summer, or in having deeply penetrating root systems. In depressions on north slopes trees are present. Only slowly are the herb communities succeeded by trees on north slopes and by shrubs on the south.

LITERATURE CITED

Abrams, Leroy. 1923. An illustrated flora of the Pacific States. **1**: Stanford Univ. Press.

Braun-Blanquet, J. 1932. Plant sociology. (Translation by Geo. D. Fuller and Henry S. Conard.) New York.

Brosnan, C. J. 1935. History of the state of Idaho. New York.

Coulter, J. M., and A. Nelson. 1909. New manual of botany of the Central Rocky Mountains. New York.

Hitchcock, A. S. 1935. Manual of the grasses of the United States. U. S. Dept. Agr. Misc. Pub. **200**.

Horton, R. E. 1921. Results of evaporation observations. Mo. Weather Rev. **49**: 553-566.

Irving, W. 1839. Astoria; or enterprise beyond the Rocky Mountains. 440 pp. London. (First published in 1836.)

———. 1843. The adventures of Captain Bonneville, U. S. A. in the Rocky Mountains of the far west. 358 pp. New York. (First published in 1837.)

Livingston, B. E., and R. Koketsu. 1920. The water-supplying power of the soil as related to the wilting of plants. Soil Sci. **9**: 469-485.

Russell, I. C. 1902. Geology and water resources of the Snake River plains of Idaho. U. S. Geol. Surv. Bull. **199**.

Rydberg, P. A. 1917. Flora of the Rocky Mountains and adjacent plains. (Publ. by the author.) Lancaster.

Sargent, C. S. 1921. Manual of the trees of North America. New York.

Stearns, H. T. 1930. A guide to the Craters of the Moon National Monument, Idaho. Caldwell, Idaho. (Reprinted from Bull. Idaho Bureau Mines and Geology. **13**. 1928.

Tidestrom, Ivar. 1925. Flora of Utah and Nevada. Contrib. U. S. Nat. Herb. **25**.

Transeau, E. N. 1905. Forest centers of eastern North America. Amer. Natur. **39**: 875-889.

U. S. Dept. Agr. 1926. U. S. Weather Bur. Bull. W. 2d ed. **1**: Sec. 22.

Verhoogen, Jean. 1937. Mount St. Helens a recent Cascade volcano. Univ. Calif. Pub. Bull. Dept. Geol. Sciences. **24**: No. 9.

Weaver, J. E., and F. E. Clements. 1929. Plant ecology. New York.

VARIATIONS IN THE HEART RATE OF BIRDS: A STUDY IN PHYSIOLOGICAL ECOLOGY

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Contribution No. 38 from the Baldwin Bird Research Laboratory and No. 574 from the Zoological Laboratory of the University of Illinois, Urbana, Illinois.

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VARIATIONS IN THE HEART RATE OF BIRDS: A STUDY IN PHYSIOLOGICAL ECOLOGY

INTRODUCTION

Although the study of physiology quite logically is concerned at first with the study of the functions of various parts, organs, and systems as separate units, the ultimate aim is an understanding of their function in the organism as a whole. Furthermore, it is the physiology of the whole organism that is of the greatest interest to the ecologist in understanding how organisms are related to and function in their environment. The measurements of rate of metabolism by various methods, rate of growth, body temperature, and rate of activity of many kinds have been extensively used in this connection because such measurements give a picture of the sum total of internal activity and provide a means of studying the effects of the environment on the entire organism.

In higher animals the rate of heart beat has long been known to be an instantaneous and very sensitive index to the general physiological condition of the whole animal. Much studied in man and laboratory animals, the heart rate has received little attention in wild species because of the difficulty of measuring it without greatly disturbing the animal. With the development of a new method of recording herein described, this difficulty has been alleviated to a considerable extent, opening the way for a more accurate study than was heretofore possible. Broadly speaking, the objects of this study are: (1) to determine the nature of the heart rate in small birds; (2) to determine the relation of the heart rate to other physiology-of-the-whole measurements, particularly, rate of metabolism, rate of breathing, and muscular activity; (3) to determine what the heart rate will reveal about the responses of birds to environmental conditions, particularly temperature. Specifically, work was conducted along three main lines: (1) laboratory study of the heart rate of nestling house wrens; (2) laboratory study of the heart rate of common species of juvenile and adult birds; (3) field study of the heart rate of wild birds in nature. In the study as a whole the primary interest has been in the physiology of the intact wild bird rather than in the functioning of the heart as an organ. An attempt has been made to combine the methods and viewpoints of the laboratory physiologist and the field ecologist and thus to bridge the all too wide gap between animal physiology and animal ecology.

Most of the experimental work was performed during the summers of 1936-38 at the Baldwin Bird Research Laboratory, Gates Mills, Ohio. The calculation of rates from the graphic records, and some additional experimentation was done at the University of Illinois. The line of work was continued at the Edmund Niles Huyck Preserve, Rensselaerville, N. Y., during 1939-40 and at the University of Georgia, but for the most part these later results are not included in this paper.

The writer is especially indebted to Dr. S. Prentiss Baldwin, recently deceased, founder and director of the Baldwin Bird Research Laboratory for the opportunity to conduct this work while acting as an assistant in the Laboratory, for financing the construction of the apparatus, and for his constant helpful criticism and encouragement. He is also greatly indebted to Dr. S. Charles Kendeigh who suggested the problem and who has given freely of his time and advice during the course of the work at the Baldwin Bird Research Laboratory and at the University of Illinois.

Appreciation is also expressed to Dr. Victor E. Shelford for his guidance in ecological work and for his many helpful suggestions, and to Dr. F. R. Steggerda for critical consideration of the manuscript. Without the aid of my wife, Martha, much of the data could not have been compiled. Acknowledgment is also due Dr. Russell A. Huggins, Dr. Paul Visscher, and other members of the Department of Biology of Western Reserve University for suggestions and the loan of equipment.

LITERATURE

There is very little literature dealing directly with the heart rate of birds, and most of this concerns a few domestic species. In wild birds the heart rate is practically unknown, and the few measurements which have been recorded are of an incidental nature with little or no control of environmental or physiological factors.

Buchanan (1909, 1910) made a few measurements on wild birds in England as well as on several domestic birds. Birds were suspended in a cloth saddle and heart rate taken by means of a capillary electrometer (early electrocardiograph) with leads from the bill and feet. Average rates per minute of wild birds obtained were: European goldfinch, 920; English sparrow, 800; greenfinch, 740; and for tame birds: canary, 1,000; pigeon, 185; parrot, 320; chicken, 330. She also pointed out the relation of heart rate, metabolism, and heart size in these birds; the formula devised, however, is of little value because the heart rates are obviously those of excited birds and therefore unstable and unreliable for comparison.

Stubel (1910) measured heart rate of several larger wild birds (hawks, ducks, etc.) in connection with blood pressure measurements. Here disturbance factors were even greater than in Buchanan's study. Koppanyi and Dooley (1928) made an interesting study of the effect of apnea on the heart rate and blood pressure accompanying diving in the domestic duck. Apnea, produced by submerging or dorsoflexing the neck caused a rapid slowing of the heart from 120-312 to 12-15 per minute within 15 seconds,

thus demonstrating a remarkable response supposedly resulting in the conservation of oxygen while under water.

Boas and Landauer (1933) compared the heart rate of the frizzle fowl with that of a normal fowl. The frizzle fowl is a variety with scanty plumage and permanent high basal metabolism as a result of high heat loss. Rates were taken while the chickens lay quietly on their backs by means of subcutaneous needle electrodes and an electrocardiograph. Minimum rates under these conditions were distinctly higher (27% in females, 68% in males) in frizzle than in normal fowls. There was no appreciable difference in newly hatched chicks of the two varieties, thus indicating that the response to scanty plumage occurs within the lifetime of the individual. The frizzle birds also respond with increased sized hearts and greater amount of hemoglobin in their blood.

Bogue (1932) has made a study of heart rate in the chick. He obtained rates of the embryo without opening the egg by inserting electrodes into the egg (but not into the embryo) and also obtained rates of chicks under anesthesia. The heart rate rose from 149 per minute at one day incubation to about 240 at 12 days incubation where it remained constant until 19 days. On hatching, the rate increased to 300 and seemed to remain at about this level which was also considered to be the adult level. Romanoff and Sochen (1936) studied the effect of temperature on heart rate of embryonic chicks finding that temperature has less effect with increasing age, indicating a transition from a cold-blooded to a warm-blooded state.

A number of measurements have been made on the domestic fowl and pigeon (see Groebbels, 1932), but the conditions under which measurements are made are rarely considered. Woodbury and Hamilton (1937) in connection with blood pressure studies in which they injected a small canula into the vessels, recorded the heart rate of the English sparrow as 550; starling, 388; and robin, 570 per minute.

APPARATUS

The Development of a Piezo-Electric Recording Apparatus

The piezo-electric principle is utilized in the apparatus devised for this study. Certain crystalline substances, particularly Rochelle salt (Na-K-tartrate), have the unique property of producing a minute electric current proportional to the pressure applied to the crystal and conversely of producing motion proportional to current passing through it. By the use of such crystals and an amplifier, it is thus possible to construct a system whereby very slight variations in pressure, vibrations, or similar motion can be amplified and recorded on moving paper and the frequency determined. It has been found that the slight motions or "jars" of the body produced by each heart cycle can be picked up and recorded by such a piezo-electric system. While piezo-electricity has been known for over a century and has been put to many uses (especially in the field of sound reproduction), it has not been utilized previously to study the heart beat of animals, and is only recently being utilized in the recording of human heart sound and electrocardiograms.

The first "piezo-cardiograph" for use with birds was built about 8 years ago by Roscoe Franks at the Baldwin Bird Research Laboratory using crystals manufactured by the Brush Development Company, Cleveland, manufacturers of piezo-electric devices. This instrument was very bulky, battery operated, and equipped with a photographic recorder. Some preliminary results were obtained with it, but it was never satisfactory for quantitative work. As a result of the development of a new pen recorder by the Brush Company and other technical advances, it became possible to build a much more suitable and portable instrument in 1937. The writer worked with the old set-up for a summer and instigated the construction of the new one described below. He is indebted to the research members of the Engineering Department of the Brush Development Company for their close cooperation and especially to Mr. C. H. Tower for frequently giving his time and advice and to Mr. Joseph J. Neff who designed the amplifier and built the apparatus. The apparatus has been designated as a "cardio-vibrometer" or simply, "vibrometer," literally, "an instrument recording vibrations."

The Cardio-Vibrometer

A description and simplied diagram of the cardio-vibrometer has already been published (Odum and Kendeigh, 1940). Photographs of the apparatus and its various modifications in use are shown in Plates I and II, Figures 15-22. As illustrated in Figure 15, the vibrometer consists of 3 separable and portable units: (1) the pickup, (2) the amplifier and (3) the recorder. The pickup unit most used was the "perch crystal" which consists of a perch lever attached to a large sensitive crystal enclosed in a metal case (for electrical shielding) and suspended from a frame by rubber bands to reduce interference from outside vibrations. Use of this pickup in both laboratory and field is illustrated in Figures 17, 18, 19, and 21. A direct "stethoscope type" pickup (Fig. 20) was also used, particularly in determining maximum rates. This was held directly against the bird and the heart beat was thus obtained. The amplifier consists of 3 stages resistance capacity coupled, is adapted to respond to low frequencies, and has a gain of about 10,000.

Details in the construction of the recorder are shown in Figure 16. The large crystal (in a sealed case) drives a light aluminum pen which writes on moving paper. The paper drive is operated by a synchronous motor which had a constant speed regardless of voltage fluctuations in the power line. Although no timer was needed, the paper speed was checked at intervals by allowing 60 cycle current to pass through the crystal and also with a stopwatch. The recorder is very sensitive and will respond to vibrations up to 90 per second. It has a distinct ad-

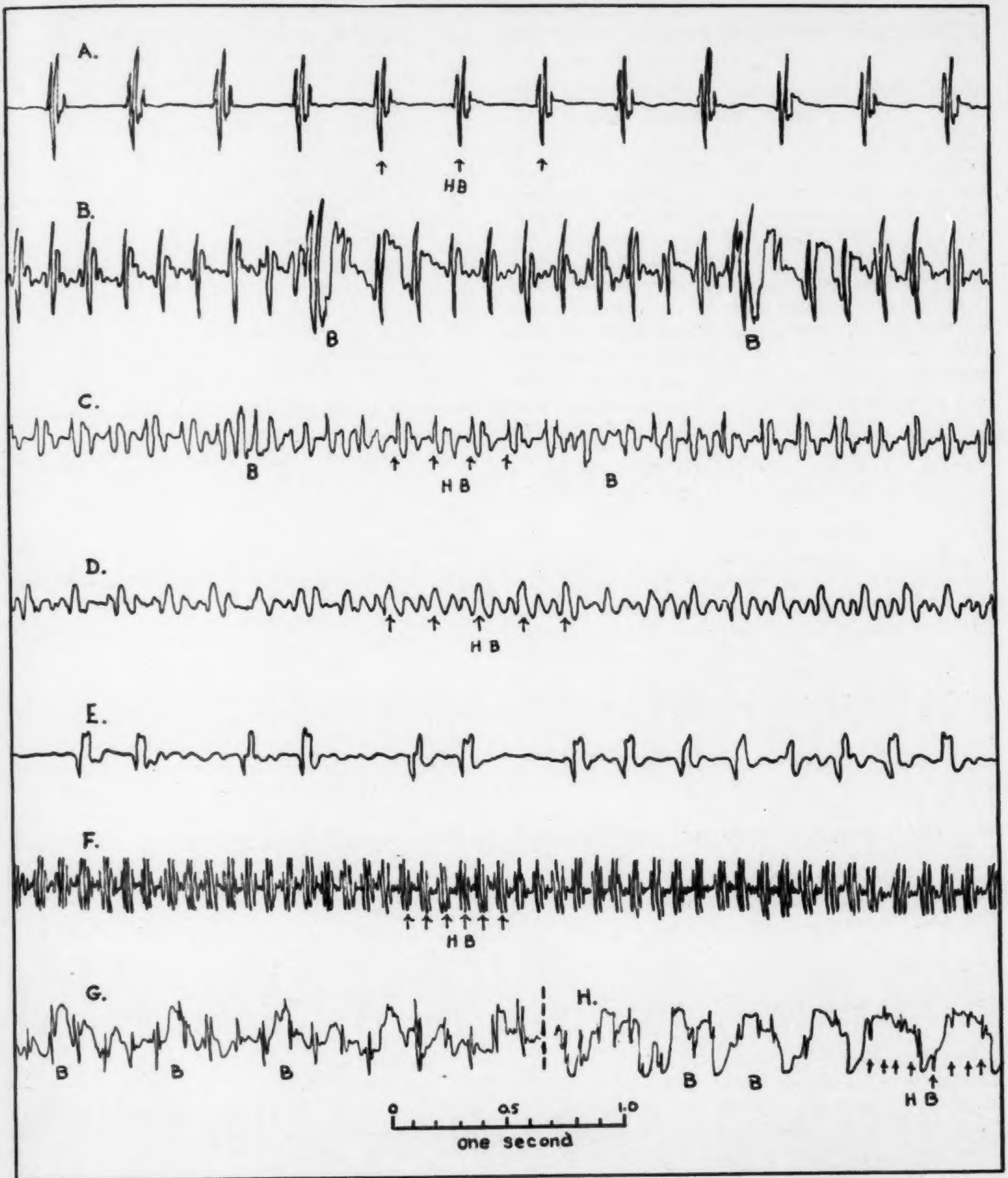

FIG. 1. Cardio-vibrograms of adult birds. HB indicates heart beat; each conspicuous stroke (indicated by arrows) represents one heart beat or a peak in a cardiac cycle. B indicates deflections due to breathing. A. Mourning dove at standard conditions; rate 172 per minute. B. Juvenile robin at standard conditions showing breathing as well as heart beat. C. English sparrow at standard conditions. A "spike-wave" type of recording; a sharp peak followed by a rounded wave occurs with each heart cycle. Breathing is indicated by the periodic blurring of the heart beat tracings. D. English sparrow at standard conditions. Vibrations are here "dampened" so that no sharp peak occurs, only the rounded wave. Note that the rate at the beginning of tracing is about 303 per minute and about 340 at the end, which illustrates the rapid spontaneous changes which normally occur in small birds. E. Typical example of sinus arrhythmia accompanying a low standard rate in a captive English sparrow; slow irregular beats alternate with rapid fairly regular ones. F. Ruby-throated hummingbird at standard conditions illustrating a very rapid and forceful heart beat; rate 645 to 727 per minute. G. Tracing obtained by use of direct stethoscope type of pickup; rapid rate of English sparrow following exercise; compare with C and D. The heart beat is here superimposed on deflections due to breathing. H. A similar direct record of a northern yellowthroat; the maximum rate is about 900 per minute.

vantage over the photographic type of recorder in that records are immediately available without time consuming and expensive film development.

CHARACTER OF THE GRAPHIC RECORDS AND METHODS OF COMPUTING THE HEART RATE

Samples of actual records obtained with the vibrometer are shown in Figures 1 and 2. The tracings are neither electrocardiograms nor heart sound records but represent the movement of the perch or crystal arm as a result of the transmission of motion of the heart via the body and feet. Therefore, records should be designated as "cardio-vibrograms." Typically, there is a sharp peak deflection or a diphasic wave or there may be a double peak with each heart cycle. The form of the curve varies a good deal according to the type of bird, its position on the perch, and the setting of the amplifier. The various forms, therefore, probably do not indicate differences in the actual beating of the heart but indicate differences in the way in which the beat is picked up and transmitted by amplifier to the recorder. Thus, in young nestlings which rest on their chests, a tracing such as shown in Figure 2, A-C, may be obtained representing the movement of the chest wall rather than the movement of the whole body and consequently resembles the "apex beat" or "cardiac impulse" of human cardiology. The clearest records are obtained when the bird is perched as in Figure 19. Doves, because of their short legs, sit close to the perch and give excellent records (Fig. 1A). Birds with longer legs do not always give such good records because they are continually balancing or teetering on the perch; this difficulty may sometimes be overcome

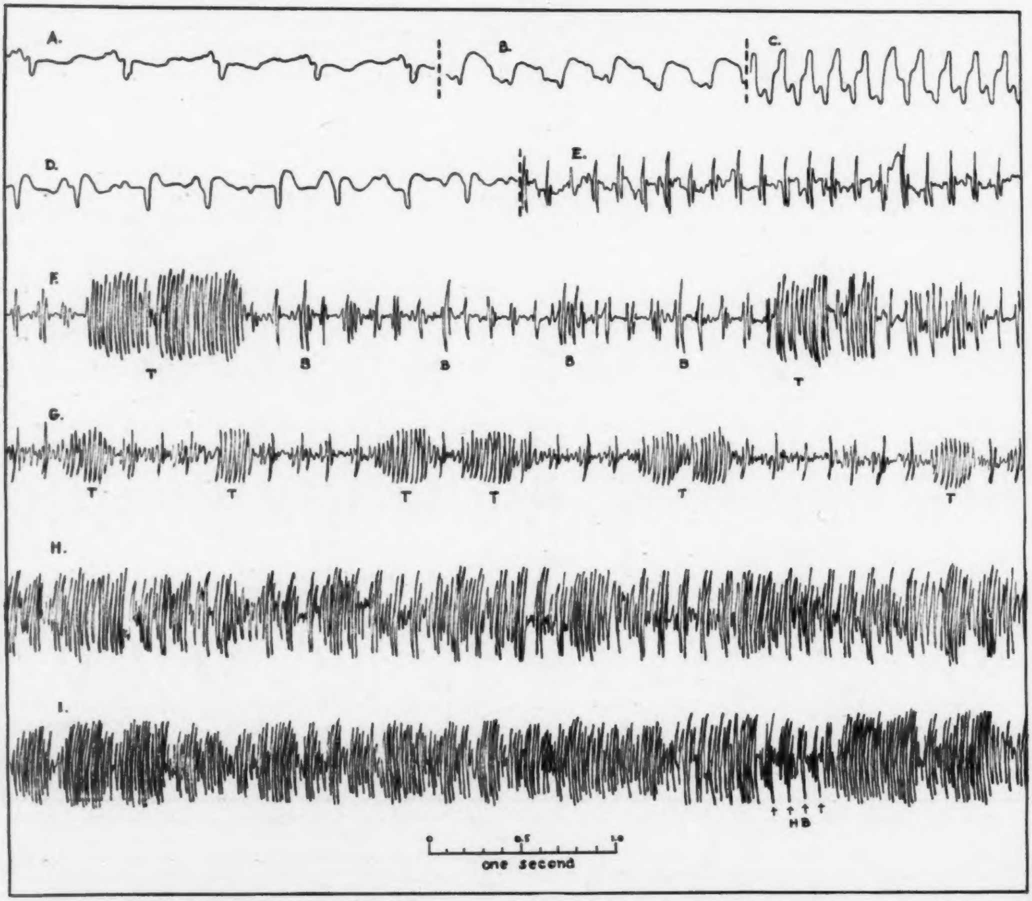

FIG. 2. Cardio-vibrograms of nestling house wrens. Heart beat and breathing indicated as in Fig. 1. T indicates muscle tremors. A-C. Records of a newly hatched bird at 70°, 80°, and 90° F. The rate and amplitude increases with increasing temperature. These types of tracings are obtained with young birds when the chest rests directly on the crystal arm. D and E. Records of a 3-day bird at 70° and 95° F. Note arrhythmia at 70° which disappears at 95°. Note also absence of tremors in 0- and 3-day birds at any temperature. F. Periodic tremors in a 6-day bird at 95° F. Breathing and heart rate are also indicated. G-I. Records of a 9-day bird at 95°, 80°, and 70° F. As temperature decreases the heart rate increases markedly and the tremor periods increase in frequency and intensity. At 70° tremors are nearly continuous and obscure the heart beat.

by placing the bird on a flat surface instead of a perch. Nestlings, young chicks, and small mammals are good subjects. Each species may present its problems and require modifications of technic.

Whatever the form of the graphic record, there is almost always a clearly recognizable sharp peak or deflection of some kind with each heart cycle, and hence the rate can be measured accurately. The heart beat unlike other movements that may be recorded is nearly always quite regular. Thus, muscle tone adjustments, tremors, movements, or motions due to breathing never produce consistently regular strokes. This is important because with practice one can learn to pick out conclusively the regularly recurring heart beats in records in which there is considerable other motion recorded.

Breathing often is recorded as well as heart beat (Fig. 1). Here again the form varies with bird, position on perch, and setting of the amplifier. Commonly, breathing is indicated by variations in width of pen strokes. It is always much slower, of course, and rarely exhibits the clockwork regularity of the heart beat. Counts of respiratory movements were often made from listening in the earphones to check and supplement the recorded data. Counts of low frequency heart beat can also be made in this way, but rates of 300 and over cannot be counted with any degree of accuracy.

Muscle tremors are also readily recorded (Fig. 2) as well as any movements made by the animal. While these movements obscure the heart recording they may furnish important supplementary data on the subject. From such graphic records and knowing the constant paper speed, it is possible to calculate the heart rate from one cycle or from any number of cycles. Fluctuations from second to second or averages over longer periods can thus be calculated. Actually, it was found convenient to use 10 beats as a unit for fast rates and 5 beats for slow. A table was constructed so that it was only necessary to measure the distance covered by 10 cycles with a pair of accurate dividers and a rule graduated in fiftieths of an inch and refer to the table for rate per minute.

If it was desired to analyze a recording in detail to show all the fluctuations, the 10-beat readings were taken at such intervals as significant change took place. If averages were desired, the most accurate procedure was to count all the beats and divide by the time; this was not practical where many feet of records were made, not only because of tediousness but because it was usually not possible to make out all the beats where periodic muscle disturbances might interfere. Hence, a sample method was used. It was found that samples every 5 seconds, when averaged, gave very nearly the same result as counting and averaging all the beats; for example:

	HEART RATE PER MINUTE		
	Case 1	*Case 2*	*Case 3*
Average counting all beats ..	339	618	420
Average of 10-beat samples every 5 seconds	339	615	425

In addition to giving an accurate average, the sample method also gives some idea of variations that are taking place during the recording period. Samples as often as 5 seconds are usually necessary because of the rapid fluctuations that occur as described in the next section. For slow rates of larger birds, samples every 10 seconds or more are sufficient to obtain an average as well as to show the major fluctuations.

It might be possible in some cases to use an electromagnetic counter or a Loomis or Fleisch recorder (see Boas and Goldschmidt, 1932) and avoid tedious measurements, but since every movement by the bird is recorded by the vibrometer such automatic counting methods would not be accurate.

The experimental procedures followed in the different phases of the study differ, so that details of methods will be left for later discussion.

GENERAL CHARACTERISTICS OF THE HEART RATE OF WILD BIRDS

VARIABILITY

A very characteristic feature of the heart rate of small birds is its great variability from moment to moment. In analyzing the graphic records, it was early noticed that the rate rarely remained the same for more than a few seconds; in fact, it often seemed to be in a state of flux from beat to beat. After plotting many of these variations, it became apparent that they were not entirely random but distinctly "oscillatory" (Fig. 3), the rate tending to oscillate up

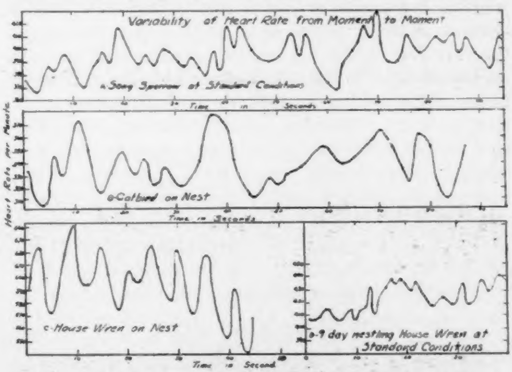

FIG. 3. Variability of the heart rate from moment to moment. Typical inherent oscillatory fluctuations in rate characteristic of small birds both under standard conditions in the laboratory and in nature.

and down even though the average rate was more or less constant.

These fluctuations are not coincident with nor apparently caused by events in the respiratory cycle. The marked oscillations in heart rate are never very regular and occur from 3 to 15 per minute in small passerine birds while the breathing rate is 40 per minute and up. Variations in heart rate due to breathing are normal in man where a slight acceleration occurs with each inspiration (Fleisch, 1932).

According to Anrep, Pascual, and Rossler (1936), this change in rate is probably a result of reflexes from the lungs acting by way of the respiratory and cardiac centers as well as possibly the "Bainbridge reflex" concurrent with the filling of the right auricle. Such a respiratory effect was noticed in some birds, but did not prove to be a universal phenomenon. If any change in rate occurs with breathing, it is momentary and lasts for only a few beats.

The degree of fluctuation varied, but may amount to as much as 20% of the average rate during a single minute (as in Fig. 3B). A common type of fluctuation consisted of a series of small variations alternating with larger ones (Fig. 3A and 3B). Individuals often exhibited a characteristic type of fluctuation; some had a strong fluctuation, or a regular one; others had a weak or irregular one. Distinct oscillatory fluctuations of one sort or another have been observed in practically all species and individuals at all levels of heart rate from low standard rates when the bird is sleeping in the dark and there is a minimum of external stimuli to high rates of active birds in nature. Therefore, it seems that such fluctuations represent a normal inherent mechanism of the heart rate which may be modified but not caused by outside stimuli. Perhaps the fluctuations are related to variations in activity of vagus nerve. Fluctuations are generally less pronounced in nestling house wrens than in adults, which is interesting in view of the fact that Bogue (1932) reports that vagus control in chicks is little developed.

Fleisch's (1932) "pulse pelotte" tracings besides showing heart rate variations due to breathing in man show a slower rhythm or a waxing and waning of the rate 2 to 3 times a minute, which would seem to be comparable to the above described fluctuations in birds. He considers a perfectly regular heart rate in man as being abnormal. A non-constant heart rate may be characteristic of at least warm-blooded vertebrates, fluctuations being more pronounced and more rapid in such highly responsive creatures as small wild birds. In considering the heart rate as an index to the effect of various factors, it is important to consider this inherent variability and to distinguish it from variations due to other causes.

THE STANDARD RATE

In order to compare heart rate of species and individuals and to better evaluate the effects of various factors, it is necessary to determine a standard or basal rate, which is the rate under standard or basal conditions. In general usage among vertebrate physiologists, "standard" and "basal" are largely equivalent terms, but "standard" is preferred for use with birds because it is a more general term whereas "basal metabolism" has come to have specialized meanings in various types of investigations and usually implies conditions of thermal neutrality. In this study, the standard rate is defined as the heart rate of the bird in a post-absorptive, but not starved condition, in darkness, away from human presence, and at any specified temperature. Riddle, Smith, and Benedict (1932) have questioned the suitability of metabolism measurements made at the zone of thermal neutrality when the object is to analyze the influence of various factors because the metabolism is abnormally depressed at this temperature. It has been found in the work with small birds that the heart rate is more constant and easier to obtain at a temperature near thermal neutrality than at lower temperatures because of the increased variability produced by muscle tremors at the lower temperatures (see later discussion). Therefore, standard rates at or several degrees below thermal neutrality seem most suitable for comparing species and individuals.

The standard rate in small passerines is apparently not maintained at a constant level for any great length of time; as the period without food continues, the rate tends to decrease gradually. This is understandable since these birds are small animals with comparatively large surface areas and little reserve energy. Figures 4 and 5 show the heart rate as

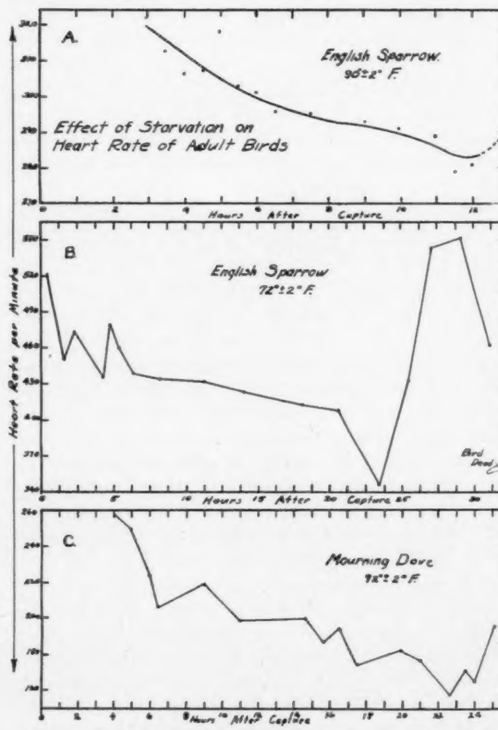

FIG. 4. Effect of starvation on the heart rate of adult birds when kept in darkness without food at a constant temperature.

affected by starvation in English sparrows, nestling house wrens of different ages, and the mourning dove. Each point represents an average of sample readings over several minutes. Figure 4A is a composite of several individuals, the other curves represent single individuals. In the English sparrow and nestling house wren, the rate decreases rather rapidly during the first 2 or 3 hours, following which the decrease is

more gradual. After continued starvation, wild birds are apt to become very restless and the heart rate, even when quiet, may be increased as indicated in several curves (Figs. 4, 5). Other experiments have shown that 2.5 hours is usually sufficient to obtain standard conditions in small passerine birds as the alimentary tract is cleared of food (Stevenson, 1933) and the respiratory quotient (in the house wren) is in the neighborhood of 0.73 (Kendeigh, 1939). While

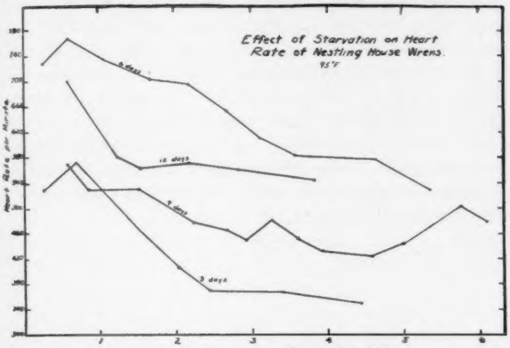

FIG. 5. Effect of starvation on the heart rate of nestling house wrens when kept in darkness without food at a constant temperature.

the heart rate usually reaches a fairly constant level after 3 hours without food, variation in 1.5 to 4 hours has been observed. Besides being slightly longer in larger species (40-50 gms.) as compared with smaller species (10-20 gms.), the variation in amount of feeding previous to capture, the amount of reserve energy (as indicated by weight), and the amount of activity during first hours of starvation are all possible factors affecting the time of reaching standard conditions. Benedict and Riddle (1929) advocate hand feeding in their pigeons so that the stomach will be filled at the beginning of the starvation period. It was not desired to introduce such a measure as artificial feeding in the study of wild birds. Rather than achieve artificially more uniform results, we were more interested in the variations that actually occurred and to interpret them in the light of the bird's physiological condition and activities in nature. The case of a female song sparrow (No. 37-93735) illustrates this point. Heart rates of this individual were taken during the night of July 6 and again in the morning of July 8 (Fig. 6); the intervening time was spent in its normal activities in the wild. After 2.5 to 3 hours, the rate was the same on both occasions; after 3.5 hours, however, the rate was maintained on the 6th but dropped rapidly on the 8th. This would seem to be due to a difference in physiological condition. In the evening the bird is at its maximum weight (Baldwin and Kendeigh, 1938) while in the morning it is near the minimum. Accordingly, in the morning before the bird has had a chance to feed its energy reserves are lowest and this may explain why the heart rate was not maintained at a more constant level.

The point to emphasize is that the "plateau" of the curve of heart rate reached after the effects of food and activity have disappeared or diminished is a sloping one and not a horizontal one. That a downward trend of standard metabolism probably occurs also is indicated by recent measurements in the domestic fowl (Barrott, Fritz, Pringle, and Titus, 1938) in which the rate of metabolism gradually decreased throughout a 3-day starvation period. Since small birds can live only 2 days or less without food, the decrease might be expected to be more rapid.

In the mourning dove, the situation is different as these birds, like the domestic fowl, possess a crop in which considerable food may be stored. Riddle, Smith, and Benedict (1932), in measurements of the standard metabolism of this species (raised in captivity),

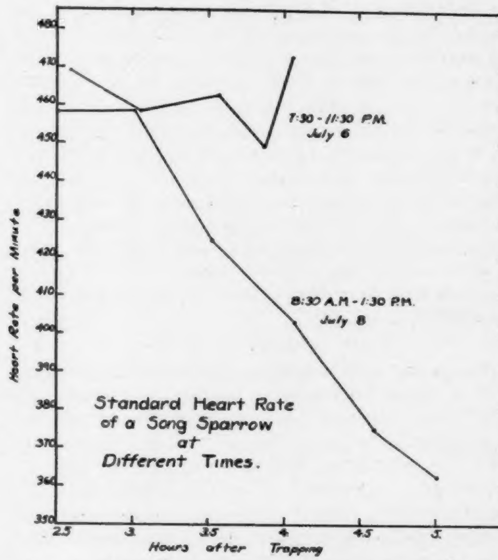

FIG. 6. Standard heart rate of a female song sparrow in the morning as compared with standard rate of same birds under the same conditions in early evening.

used a 24-hour starvation period to correspond to the period necessary in the larger ring dove and pigeon, but state that standard conditions, as indicated by the R.Q., could probably be obtained 4 or 5 hours earlier. In wild doves, what would seem to correspond to the sloping plateau of the curve of small passerines seems to be reached in 8-10 hours (Fig. 4C), since the rate from this point to 24 hours decreases but little as shown in the following three individuals:

	HEART RATE PER MINUTE		
	No. 1	*No. 2*	*No. 3*
8-10 hours without food	210	220	156
18 hours without food	185	200	143
24 hours without food	175	190	...

After 24 hours or less, the wild doves tend to become restless so that the heart rate may be less constant than that obtained earlier.

With all birds it is important to specify the time of day in which the standard rates are taken because even under constant experimental conditions, the various daily rhythms (activity, weight or energy reserve, body temperature) which occur under natural conditions may affect directly or indirectly the heart rate.

HEART RATE OF NESTLING HOUSE WRENS IN RELATION TO AIR TEMPERATURE AND THE DEVELOPMENT OF TEMPERATURE CONTROL

Nestling house wrens were worked with intensively in order to obtain a knowledge of the relation of the heart rate to changes in temperature regulation which occur during development. This is important in understanding the physiological mechanisms involved in the responses of birds to environmental temperature, and it may also have considerable phylogenetic significance since nestlings of an altricial species, such as the house wren, pass from the poikilothermic condition found in lower vertebrates to a homoiothermic condition of higher vertebrates within the short time of their nest life. In addition, concurrent measurements of the rate of metabolism by Dr. S. C. Kendeigh offered an opportunity to compare heart rate with metabolism under the same conditions. Finally, nestling wrens were available in numbers and were less difficult to work with than the adults.

METHODS

Six ages of birds were used, just hatched or 0 days, 3, 6, 9, 12, and 15 days of age (ready to leave the nest). The standard heart rate of these ages was determined at 6 temperatures, 70° F. (21.1° C.), 80° F. (26.7° C.), 90° F. (32.2° C.), 95° F. (35.0° C.), 100° F. (37.8° C.), and 105° F. (40.6° C.). The technic used to obtain the heart rate of nestlings was as follows: the nestling was placed in a small pasteboard box attached to the crystal perch (Fig. 21). Different sized boxes were used to correspond to the size of the nestlings. These boxes were open above, had holes in the sides to insure circulation of air and had sloping bottoms (20-30° incline). The sloping bottom imitates the natural concavity of the actual nest and was an important feature in maintaining the bird in a comfortable position. If the nestling was uncomfortable, excessive struggling occurred which made records difficult to obtain as well as untrustworthy.

The crystal, the box, and the bird were contained in a constant temperature chamber (Fig. 20). The walls of the chamber were made of an inner layer of asbestos, a ¾ inch layer of insulating material (both for heat and sound), a metal layer, and an outside wood layer. The metal layer was grounded and the crystal shielded from electrical disturbances, although this precaution was not not always necessary. Heat was supplied by two quick-acting resistor type heaters with metal shields to prevent direct radiation towards the bird. The temperature was controlled by a bimetallic DeKhotinsky thermoregulator in the top of the box. The chamber was located in a basement dark room of the laboratory which varied very little in temperature or humidity during the day and comparatively little from day to day. A hygro-thermograph operated in the room at various times during the summer showed that the extreme temperature variations were from 65° F. (18.3° C.) to 75° F. (23.9° C.) and relative humidity variations were from 70% to 95%.

As long as the chamber was not opened, the temperature within was controlled within 1.8° F. (1.0° C.). Humidity was not controlled but because of the relatively constant conditions of the room, it varied but little at a given temperature. The relative humidity in the chamber was measured at intervals by means of a hair hygrometer, and the following were the approximate relative humidities associated with the temperatures used:

70° F.	75-85%
80° F.	55-65%
90°-95° F.	40-53%
100°-105° F.	30-40%

The procedure used in determining the standard heart rates was as follows: the bird was removed from the nest and placed in an incubator in darkness at 95° F. After 2 hours it was placed in the box on the crystal in the temperature chamber in total darkness at the desired temperature, and half an hour was allowed for adjustment to the conditions before records were taken. By the end of the 2.5 hours, the bird was at or near standard conditions as already explained. At intervals of 15 to 30 minutes during the next 1.5 to 2.5 hours, recordings of heart rate were made; each recording period, which usually lasted from 5 to 10 minutes, resulted in a number of graphic records averaging 30 seconds duration. For several minutes preceding, as well as during a recording period, the amount of activity was judged by listening in the earphones and records were made only when the bird was as quiet as it would get under the particular conditions. The standard rate for a given temperature was determined by averaging the rates obtained for each recording period. If an excessive movement occurred during a record, the rate immediately after was not included; otherwise, no attempt was made to eliminate effects of general activity. Variation in muscular activity is an important part of the response to temperature and its effects on the heart rate are perfectly normal. To take the lowest readings of each recording as the basis for a standard rate would not give a true picture of the way the bird responds to each different temperature.

Ordinarily, once placed in the temperature chamber, the bird was left undisturbed in the dark until the end of the experiment. The air temperature in the box just above the bird was checked at each recording period by means of thermocouples (Fig. 21) and a Leeds and Northrup indicator potentiometer located in another room. The room containing the chamber and bird was kept dark and quiet and

was entered only when it became necessary to adjust the thermostat.

At the end of the experiment the bird was removed, weighed, and returned to the nest. In addition, the body temperature was often taken by means of a thermocouple down the throat and the indicator potentiometer, in order to determine whether temperature control was being maintained. At first, it was thought desirable to record body temperature simultaneously with heart rate by leaving the thermocouple down the throat during the experiment, but it was soon found that this disturbance nearly always increased the heart rate, and the procedure was abandoned. As far as possible, a given individual was used only once; if used again, at least a week of normal nest life intervened.

All work with nestlings was done in the daytime; usually one experiment was run in the morning, another in the afternoon. Since the house wren at the latitude of Cleveland, Ohio, raises two broods and since 50-100 active nests were under observation, nestlings were available nearly continuously from the middle of June to the middle of August. Detailed notes on these nests were kept so that the age and history of the nestlings were accurately known. A total of 120 nestlings were used in all and about 9,000 feet of recording were made. About 3,000 readings of heart rate were calculated from this as well as over a 1,000 measurements of rate of breathing and muscle tremors.

THE RELATION BETWEEN HEART RATE AND AIR TEMPERATURE

The average standard heart rate of the 6 ages at the various temperatures is given in Table 1 and Figures 7 and 8. These particular data are based on 98 individuals, 373 recording periods, and 2,490 readings of heart rate. Nestlings which varied too widely from the average weight or general development for the age were not included. Likewise, early experiments performed before the technic had been worked out were eliminated as far as possible. Data on the older nestlings at low temperatures are meager because muscle tremors made it difficult to determine heart rate.

As has previously been shown (Baldwin and Kendeigh, 1932), the 0- and 3-day old birds are cold-blooded in that their body temperature is not maintained more than a degree or so above the air temperature. The 12- and 15-day birds, on the other hand, are virtually warm-blooded in that they tend to maintain a high body temperature with drop in air temperature. The 6- and 9-day birds are intermediate. Some idea of the physical development of the nestlings is indicated by the following table. The data on feather development are from Boulton (1927).

Age in Days	Basic Weight in gms.	Length of Body Feathers in mm
0	1.2	0.0
3	3.6	0.0
6	6.6	0.39
9	8.4	3.3
12	9.2	6.5
15	9.2	8.3
Adult	9.7	12.3

As will be seen from Table 1, there is virtually no difference in the heart rate of 0- and 3-day birds; differences are small and are not consistently higher or lower. When the data for these two ages are com-

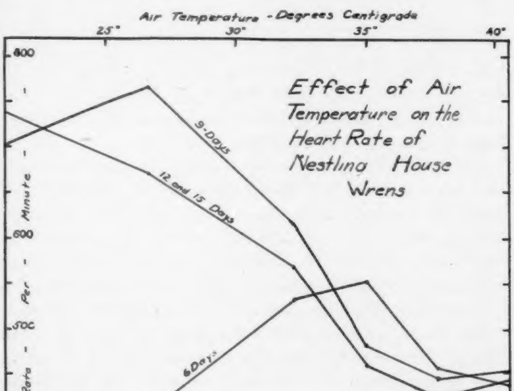

FIG. 7. The effect of air temperature on the heart rate of nestling house wrens of different ages.

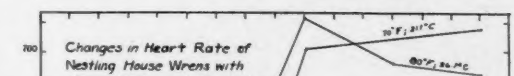

FIG. 8. Changes in the heart rate of nestling house wrens with age at different temperatures.

bined, the curve representing the temperature-heart rate relation in the cold-blooded stages of the house wren is obtained (Fig. 7). Likewise, the data for 12- and 15-day nestlings may be combined to obtain the relation in the warm-blooded stages.

The relation of heart rate and air temperature in 0- and 3-day birds is the expected one for a cold-blooded animal; the heart rate increases with an increase in air temperature and also body temperature since it varies within 1-2° F. of air temperature. The curve is similar to the heart rate-temperature curves of cold-blooded species as, for example, the frog (Barcroft and Izguierdo, 1931) or Ambystoma (Laurens, 1914). It would seem to resemble the temperature-growth or temperature-activity curves obtained with plants and various cold-blooded animals (see Shelford, 1929) which roughly consist of a sigmoid-type curve with a straight line portion at median temperatures, rather than the curve obtained with Arrhenius' formula or the Q_{10} relation, both of which are concave.

As the air temperature decreases, the strength of the beat as well as the rate decreases in the first two ages (Fig. 2A-C). Twice as much amplification is needed at 70° F. to get an appreciable deflection of the pen. The force of the beat becomes so weak below 70° F. that it was not possible to measure it with the present apparatus. "Sinus arrhythmia" or marked irregularity of beat was noted in 3 out of 7 of the 0- and 3-day birds at 70° F. and in one 3-day bird at 80° F. No arrhythmia was noted at any of the other temperatures. One individual exhibited an arrhythmic beat at 70° F. which completely disappeared when it was placed at 95° F. (Fig. 2D-E). Therefore, a disturbance of the characteristic regularity of the heart contraction is apparently associated with slow rates at low temperatures. It is probable that this tendency increases with a further drop in temperature until the heart rhythm becomes very irregular as the lower lethal temperature is approached. The lower lethal body temperature is 47-50° F. (8.3-10.0° C.). (Baldwin and Kendeigh, 1932). It should be stated here that the subjection of 0- and 3-day birds to 70° F. for several hours has no detrimental effect.

At six days of age, the temperature control mechanism is beginning to be established, and this is reflected in a considerable change in the behavior of the heart rate. At 100° and 105° F., the heart rate is about the same as in the two younger ages, but as the air temperature drops to 95 and 90° F. a considerable increase in the rate occurs even though the body temperature decreases. At 105° F., the body temperature averaged approximately 107° F., and at 95° F., approximately 97° F. The sharp increase in the heart rate is apparently a part of the mechanism attempting to maintain a constant body temperature but heat loss is so great due to the poor feather development at this age that it is inadequate. With a further drop in temperature, the heart rate decreases rapidly but is maintained at a higher level than in 0- and 3-day birds. However, individual variation at this age was great, particularly at 80° and 90° F. (Table 1) as might be expected in an intermediate stage in temperature control.

TABLE 1. Standard heart rate per minute of nestling house wrens.

	Age in days:	0	3	6	9	12	15
	Number of birds:	3	3	3	1	—	2
70°F.	Recording Periods:	10	11	9	4	—	7
21.1°C.	Average:	156	121	277	703	—	738
	Minimum:	135	112	251	676	—	698
	Maximum:	181	149	298	732	—	800
	Number of birds:	3	3	3	2	2	1
80°F.	Recording Periods:	8	12	11	7	7	5
26.7°C.	Average:	213	229	409	768	680	661
	Minimum:	199	182	215	734	600	606
	Maximum:	227	253	515	830	742	668
	Number of birds:	2	2	4	4	2	4
90°F.	Recording Periods:	11	8	20	13	8	16
32.2°C.	Average:	360	320	533	617	627	512
	Minimum:	323	278	402	498	556	427
	Maximum:	392	356	655	687	730	602
	Number of birds:	3	5	4	4	3	5
95°F.	Recording Periods:	12	18	15	16	11	20
35.0°C.	Average:	364	390	553	483	479	448
	Minimum:	308	348	491	421	418	391
	Maximum:	407	455	654	583	552	508
	Number of birds:	2	2	2	2	2	2
100°F.	Recording Periods:	9	6	10	8	7	7
37.8°C.	Average:	433	411	457	445	389	460
	Minimum:	392	350	411	393	368	427
	Maximum:	492	475	498	547	408	490
	Number of birds:	3	2	4	4	3	3
105°F.	Recording Periods:	12	7	11	14	12	11
40.6°C.	Average:	453	396	440	457	442	447
	Minimum:	426	376	414	423	370	355
	Maximum:	486	411	456	449	488	543

At 9 days of age the heart rate increases with a decrease in air temperature down to 70° F. when it decreases slightly (Fig. 5). At 12 and 15 days of age, the heart rate-temperature curve is virtually as would be expected in a warm-blooded animal; the heart rate increases with a drop in air temperature in a reverse sigmoid manner. The amount of increase at 95° F. as compared with 100° F. is less than in birds 6 days of age, and at 90° and 80° F., it is less than in birds 9 days of age. This would seem to be correlated with an increased control over heat loss due primarily to better feather development, thus relieving the strain on the blood circulation concerned in heat production.

The extent of the variation in heart rate of all these ages as a result of air temperature is rather surprising and indicates the great sensitivity of young birds to temperature changes. Sufficient data on adult house wrens are not available but judging from measurements on other species, the effect of air temperature on the heart rate of the adults is similar to the older nestlings, but the extent of the variation is less, correlated with the still greater development of the temperature control.

The temperature of the lowest heart rate or "zone of thermal neutrality" is apparently around 100° F.

for those nestlings with temperature control (9, 12, and 15 days). The lowest rate of CO_2 production also occurs at 100° F. (Fig. 9).

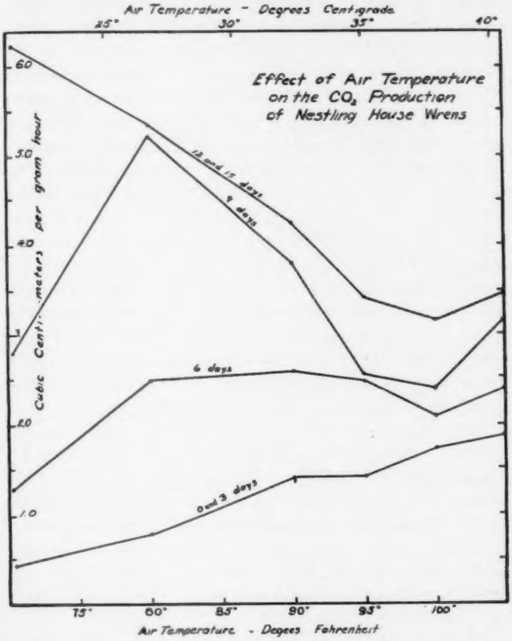

FIG. 9. The effect of air temperature on the carbon dioxide production of nestling house wrens of different ages.

Figure 8 shows the data of Table 1 plotted according to age. At lower temperatures the heart rate increases with age following a sigmoid curve. At air temperatures of 100 and 105° F., on the other hand, the heart rate remains virtually the same at all ages. At 95° F. it seems to be definitely higher at 6 days of age than earlier or later.

These heart rate-temperature relations are of considerable interest in the consideration of the conditions in nature. The nest temperatures have been extensively measured by means of thermocouples (Baldwin and Kendeigh, 1932). The temperature of the nest is not constant, of course, but varies due to the attentive and inattentive behavior of the adults and to the weather. Thus, nestling birds may be subjected to an air temperature range equal to the experimental range of 70-105° F., but for the most part, nest temperatures range from 85 to 100° F. and average 95° F. Since older birds are brooded less, they may be subjected to a wider range of air temperatures than the younger nestlings. It is interesting to note, therefore, that nest temperatures generally are close to the thermal neutral temperature.

COMPARISON OF HEART RATE AND METABOLIC RATE

Curves of the rate of metabolism as indicated by the CO_2 production of the same ages at the same temperatures are shown in Figure 9 (from data by Kendeigh, 1939). Comparable procedures and the same source of material (but not the same individuals) were used as in the heart rate studies, except that the relative humidity in the bird chamber of the metabolism apparatus was much lower, being from 8 to 16%.

The two sets of curves (Figs. 7, 9) are strikingly similar showing that there is a definite relation between heart rate and metabolic rate as might be expected. The most significant difference seems to be that the rate of metabolism per gram-hour at thermal neutrality (100° F.) increases with age whereas the heart rate (per individual) is virtually the same for all ages. If the relative heart size (heart weight per unit of body weight) decreases with age in the wren as it does in the chick (Mitchell, Card, and Hamilton, 1932), it would seem that since the heart rate remains the same, the stroke volume per unit of tissue actually decreases with age, even though the metabolic rate increases. Kalabukhov and Rodionov (1934) have shown that the erythrocyte number and hemoglobin content of the blood of the English sparrow (an altricial species like the wren) nearly doubles between the ages of 1 and 15 days. Also, the breathing rate in wrens seems to increase with age (Fig. 11). Thus, the increased efficiency of the blood and possibly increased ventilation may explain how an increase in metabolism per unit weight can occur with age even though the output of the heart per unit weight decreases.

There are several other differences in the curves which may or may not be significant. The rate of CO_2 production in 6-day birds is maintained rather constant from 80 to 105° F. whereas the heart rate increases markedly at 90 and 95° F. The increase in CO_2 output at 105° F. is small but definite, whereas the increase in heart rate is scarcely perceptible.

MUSCLE TREMORS

The vibrometer has proved to be excellent for detecting and recording muscle tremors or shivering movements; in fact, tremors have been an obstacle in recording the heart beat of the warm-blooded birds at low temperatures. The sensitivity of the instrument is such that tremors can be detected even though no shivering is observed with the eye. While most of the recordings in this study were made primarily for determination of heart rate, a considerable amount of data on tremors were accumulated at the same time, and their importance in the development of temperature regulation quickly appreciated.

Figures 2F and 2H illustrate the way in which tremors develop with falling air temperature. At higher temperatures, tremors commonly occur in short periods often less than a second in duration alternating with longer periods without discernible tremors. At lower temperatures, tremor periods become longer and non-tremor periods less frequent. Even when tremors are continuous their frequency often varies in a more or less cyclic manner.

Tremors have considerable effect on the heart rate as would be expected since they are in reality a form

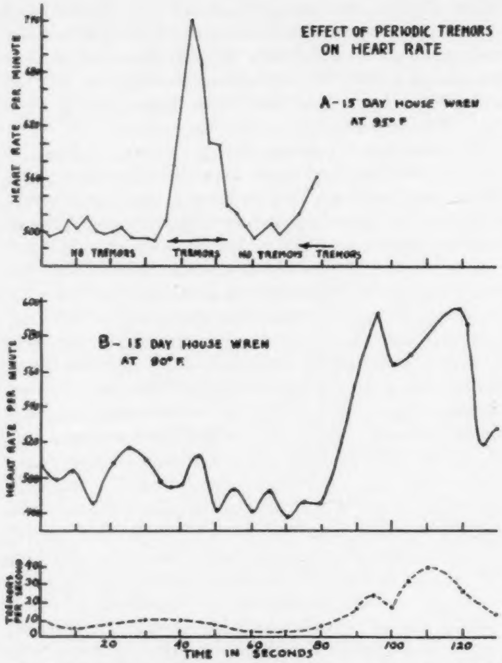

FIG. 10. The effect of periodic tremors on the heart rate of nestling house wrens.

of muscular activity (Fig. 10). If tremors are continuous, the heart rate tends to remain at a high level; if tremors are periodic, the rate tends to fluctuate from one level to another. Very brief tremor periods, on the other hand, often have little or no immediate effect on the heart rate.

Table 2 gives in a quasi-quantitative way measurements of tremors at different ages and temperatures. Since tremors often do not occur continuously, several factors are involved: (1) frequency, (2) duration, and (3) intensity. By "number of tremors per second" is meant the number of vibrations transmitted to the crystal by the entire body as determined by taking 1-second sample readings at 5-second intervals. Periods when no tremors occur are thus included in the averages along with active periods in something of the proportion of their occurrence. "Percent tremors present" indicates the approximate portion of time when the bird is undergoing unmistakable tremors: 100% indicates it is shivering continuously; 50%, shivering half the time and half not. Even where tremors are continuous (100%), their frequency often varies in a more or less cyclic manner. No attempt was made to measure the intensity or force of the tremors but the impression gained is that intensity increases with an increase in frequency and duration.

TABLE 2. Variation in muscle tremors in nestling house wrens.

	Age in days:	6	9	12	15
	Number of birds:	3	1	1	2
70°F.	Average No. per second:	24	37	35	34
21.1°C.	Per cent time present:	80	100 (–)	100 (–)	100 (–)
	Number of birds:	2	2	2	2
80°F.	Average No. per second:	29	30	34	30
26.7°C.	Per cent time present:	92	96	93	95
	Number of birds:	2	3	2	3
90°F.	Average No. per second:	17	16	21	8
32.2°C.	Per cent time present:	24	26	45	28
	Number of birds:	2	2	2	2
95°F.	Average No. per second:	3	5	7	3
35.0°C.	Per cent time present:	10	7	12	8
	Number of birds:	2	2	2	2
100°F.	Average No. per second:	1	5	3	4
37.8°C.	Per cent time present:	3	10	5	7
	Number of birds:	2	2	2	4
105°F.	Average No. per second:	0	0	0	0
40.6°C.	Per cent time present:	0	0	0	0

No tremors whatsoever could be detected in 0- and 3-day birds. Tremors first appeared in the 6-day-old stage which is significant since temperature control is first becoming apparent. It appears that tremors are an important source of heat production and are certainly concerned in the acceleration of the heart at low temperatures. The cold-blooded birds exhibited no tremors and consequently do not have this means of increasing heat production to produce a body temperature greater than the air temperature. Six-day and all older birds, on the other hand, produce muscle tremors and exhibit increased heat production, heart rate, and body temperature.

The frequency and duration of muscle tremors in-

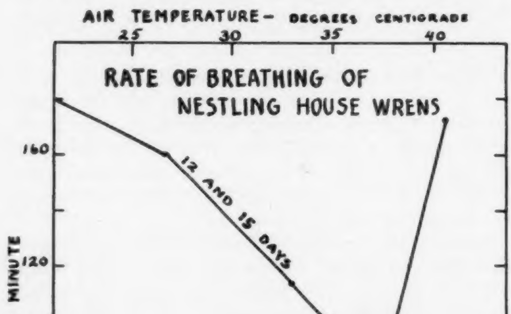

FIG. 11. The effect of air temperature on the rate of breathing of nestling house wrens in the poikilothermic (0 and 3 days) and the homoiothermic (12 and 15 days) stages.

crease with a drop in temperature in 9-, 12-, and 15-day old birds (Table 2). At 6 days of age, tremors appear to be less at 70° than at 80° and 90° F. Also, they are somewhat greater in 9- and 12-day birds than in 15-day birds, perhaps to be correlated with high heat loss and greater need for heat production. In general, therefore, tremors are directly correlated with heart rate.

In adult and juvenile birds, tremors tend to be less frequent under comparable temperature conditions. Thus, tremors are absent or slight in adults at 95° F. and they are normally only periodic at 70° F. if detectable at all.

Rate of Breathing

The rate of breathing in the cold-blooded nestlings (0- and 3-days) increases with an increase in air temperature the same as does heart rate (Fig. 11). Likewise, breathing rate increases with a drop in air temperature in warm-blooded wrens (12- and 15-days), but it also increases greatly at 105° F. in contrast with the heart rate which shows only a slight increase. In one 12-day bird, the increase at 105° F. was especially marked as breathing became a rapid panting, varying from 200 to 360 per minute, while at the same time the heart rate was only 450 to 480 per minute.

TABLE 3. Standard rate of breathing per minute in nestling house wrens.

	Age in days:	0 and 3	12 and 15
	Number of birds:	5	1
	Number of readings:	12	1
70°F.	Average:	7.6	180
21.1°C.	Minimum:	3.1	—
	Maximum:	13.9	—
	Number of birds:	3	2
	Number of readings:	6	6
80°F.	Average:	11.1	159
26.7°C.	Minimum:	8.3	140
	Maximum:	13.1	181
	Number of birds:	2	2
	Number of readings:	5	2
90°F.	Average:	27	120
32.2°C.	Minimum:	22	96
	Maximum:	34	144
	Number of birds:	7	8
	Number of readings:	16	15
95°F.	Average:	34	96
35.0°C.	Minimum:	23	80
	Maximum:	49	120
	Number of birds:	2	3
	Number of readings:	7	3
100°F.	Average:	55	93
37.8°C.	Minimum:	46	92
	Maximum:	68	96
	Number of birds:	5	4
	Number of readings:	13	13
105°F.	Average:	55	172
40.6°C.	Minimum:	36	125
	Maximum:	73	360

With high air temperatures, the necessity of heat loss becomes paramount. Since birds do not have sweat glands, the lungs and air sacs are the principal means of heat loss. Measurements of water loss made in metabolism experiments (Kendeigh, 1939) showed that the water loss at 105° F. was twice as great as at 100° F., while water loss at 70° F. was about the same as at 100° F. It would seem, therefore, that variations in breathing rate serve two distinct functions. At high temperatures, increase in breathing is primarily concerned with heat loss while at low temperatures, an increase is concerned with the oxygen supply required in increased heat production.

THE HEART RATE OF ADULT AND JUVENILE BIRDS

The results obtained with adult and juvenile birds are intended to be only of a survey nature. Since there is very little information on the heart rate of any wild birds, it was thought desirable to touch on various aspects rather than concentrate on any one. Much of the following data is suggestive rather than conclusive. Juveniles are those birds which have left the nest and become independent of their parents but have not undergone the fall molt. Adults are those birds that have reached a breeding state, which in passerine birds usually means that they are one year or more old.

Methods

Baited traps designed to capture birds uninjured for banding purposes were operated continuously on the sanctuary surrounding the laboratory. Birds were collected from the traps at 2-3 hour intervals, brought to the laboratory, weighed, examined, banded, and released. Birds to be used in experiments were simply detained for the desired period. Only freshly taken and healthy birds were used as a rule, the idea being to measure as nearly as possible the normal wild condition. In most cases, birds had been engaged in feeding around or in the traps up to a short time of capture. Since all birds were banded with Biological Survey aluminum bands, their individuality was known.

The procedure used in determining standard rates was the same as used with nestlings, except the bird was allowed to sit on a perch (Fig. 19) instead of being placed in a box. To get wild birds to sit contentedly on a perch was accomplished with most species and individuals through the use of a box 8.75 x 5 x 8 inches with a glass top so constructed and arranged that the perch of the perch crystal projected into it from the side. The bird was placed in the box in total darkness and a flashlight directed on it from above. As a result of the light, the bird usually hopped up on the perch, or in its attempt to get out of the glass top, soon came to rest on the perch, at which moment the light was turned off. Once established on the perch, the bird usually remained there indefinitely as long as it was dark and quiet, although it was free to move around on the perch. Thus, the bird was in a natural position and its activity restricted without the necessity of

placing it in cramped quarters. For doves it was found that no restraining box was needed as these birds will stay on the perch if placed there gently in the darkness. At least 45 minutes, usually an hour, was allowed for it to settle down and become adjusted to the conditions before records were taken. During this period, the bird's behavior was checked at intervals by means of the earphones.

Comparison of the Standard Rates of Species

The results of standard rate determinations of 13 species, 36 individuals are shown in Table 4. The data are based on about 2,500 sample readings or about 67 readings for each individual.

TABLE 4

Species	Age and sex		Weight at capture gms.	Date	Time of capture	Recording interval hours after capture	Standard heart rate per minute	Variation in rate per minute
Mourning dove......	Adult		120.5	July 4–5	5:00 P.M.	14–24	*182**	157–200
"	"		152.0	July 4–5	4:30 P.M.	14–18	*152*	144–163
"	"		128.9	Aug. 18–19	6:00 P.M.	14–24	*199*†	182–215
"	"		135.6	Aug. 13–14	4:30 P.M.	14–24	*216*†	190–240
"	"		121.3	June 20	2:30 P.M.	8–10	159	146–171
English sparrow....	Juvenile		29.4	July 3	6:00 P.M.	3–5	323	318–330
"	Adult	♂	28.0	June 28	6:30 P.M.	3–5	303	289–324
"	Adult	♀	29.9	July 10	11:00 A.M.	4½–6	*378*	367–393
"	Adult	♂	31.0	July 2	7:15 P.M.	3½–4½	305	297–315
"	Juvenile		26.1	June 29	8:30 A.M.	3–6	*352*	326–425
"	Adult	♂	—	May 10	5:30 P.M.	3–5	356†	337–394
"	Juvenile	♂	—	Aug. 16	11:45 A.M.	3–5	*458*†	436–480
Song sparrow....	Adult	♀	17.5	July 6	7:30 P.M.	3–4	463	445–479
"	Juvenile		19.9	Aug. 20	8:40 A.M.	2½–3	*454*	442–473
"	"		21.8	Aug. 23	2:50 P.M.	2–4	388	377–398
"	"		18.5	Aug. 26	11:35 A.M.	3–4	*571*	554–598
"	"		19.7	Aug. 26	11:35 A.M.	2–3	*386*	379–393
"	Adult		22.3	May 17	5:00 P.M.	3–5	401†	391–410
House wren......	Adult	♂	10.6	Aug. 2	7:00 P.M.	2½–3½	455	449–475
"	"	"	10.4	June 15	8:15 P.M.	2½	450†	426–466
"	Juvenile	♂	10.3	Aug. 25	11:45 A.M.	2½–3	*468*	460–478
"	Juvenile		10.4	July 22	12:00 Noon	3–4	*397*	368–422
"	"		10.4	July 4	12:30 P.M.	5–6	*451*	444–455
Cardinal....	Adult	♂	41.7	July 5	4:30 P.M.	4–6	391	374–429
"	"	"	41.4	July 4	5:00 P.M.	3–4	350	329–385
Towhee.....	Juvenile	♂	40.3	Aug. 26	8:30 A.M.	3–3½	*468*	464–472
"	"	"	44.0	Aug. 25	3:00 P.M.	3–4	*515*	505–538
"	Juvenile	♀	43.8	Aug. 25	6:00 P.M.	2½–4	395	380–430
"	"	"	37.7	Aug. 26	8:30 A.M.	2½–3	*416*	410–430
Black-capped chickadee..	Adult	♂	11.2	June 20	7:05 P.M.	2–3	522	484–538
"	"	"	11.1	June 21	4:30 P.M.	4–5½	531	513–560
"	"	"	11.4	June 11	6:20 P.M.	3½–5	504	484–520
Catbird.....	Adult	♂	32.1	July 14	8:30 A.M.	3–5½	*330*	318–354
Cowbird....	Juvenile		44.2	July 12	6:00 P.M.	3–5	315	288–358
Brown thrasher...	Adult	♂	77.6	Aug. 18	11:45 A.M.	2½–3½	*278*	270–294
Yellow warbler....	Adult	♀	14.0	June 19	8:00 P.M.	2½–3½	480	440–510
N. yellow-throat.....	Juvenile		10.3	Aug. 23	9:00 A.M.	2½–3	*410*	392–422
Field sparrow....	Adult		12.6	Aug. 25	8:30 A.M.	2½–3	*438*	420–470
Ruby-throat. humming-bird.......	Adult	♂	3.0	June 30	7:00 P.M.	2–3	614	550–650

**Italics* = daytime recording. † = temperature 72 ± 2°F.; all others at 92 ± 2°F.

While the data are to be considered preliminary as they are based on few individuals of any one species, they represent the first records of heart rate of wild birds under anything like comparable conditions. The rates are much lower than have been reported hitherto for small birds and the variations less. For example, the heart rate of the English sparrow has been reported as being anywhere from 550 per minute (Woodbury and Hamilton, 1937) to 800 per minute (Buchanan, 1909). While we expect considerable variation in heart rate, all records of wild birds in the literature are too high and variable to represent basal or standard rates and therefore are not reliable for comparison except in a very general way.

If possible differences due to sex and time of day are disregarded for the moment, the standard summertime rate (at 90° F.) in round numbers for several common species is as follows:

Species	*Number of Individuals*	*Weight in Grams*	*Heart Rate Per Minute*
Mourning Dove (ad.).........	3	135	165
Towhee (juv.)...............	4	40	445
Cardinal (ad.)...............	2	40	370
English Sparrow (ad. and juv.)	6	28	345
Song Sparrow (ad. and juv.)..	5	20	450
House Wren (ad. and juv.)....	4	11	445
Black-capped Chickadee (ad.)..	3	12	520
Hummingbird (ad.)...........	1	4	615

Roughly speaking, heart rate is inversely related to size. In general among homoiothermic animals, the heart rate of smaller animals is more rapid than that of larger ones in the same or related taxonomic groups (Clark, 1927). However, where small differences are concerned, the size correlation is not consistent, or necessarily proportional. Referring to the above data, it seems that the towhee and cardinal, although one-fourth larger, have a standard heart rate greater than the English sparrow. Likewise, the song sparrow is nearly twice the size of the house wren, but the standard rates of the two species are about the same. The mourning dove has a slower standard rate than that reported by Boas and Landauer (1933) for the domestic fowl, a much larger bird. Factors other than body size undoubtedly affect the comparative heart rates of species. While present information is too meager to establish any conclusions, it might be well to briefly consider some of the possibilities that may be involved.

Composition of the blood, heart size, and life habits are possible factors influencing the comparative heart rate of different species. Little is known about the relative oxygen carrying power of the blood of different species. However, a considerable number of measurements of number and size of erythrocytes have been made (Gulliver, 1876; Groebbels, 1932; Bartsch, Ball, Rosenzweig, and Salman, 1937). From these references the writer prepared a table showing the number and dimensions of erythrocytes of representative species in various taxonomic groups and calculated the approximate surface area of the cells.

The size of the red cell decreases with the size of the bird, but the number of cells per cubic millimeter increases, so that the total surface area per cubic millimeter is approximately the same in all but extreme sized birds. Erythrocytes of birds are apparently about half as numerous per cubic millimeter as in mammals of comparable size, but they are also about twice as large so that the surface area may not be greatly different in the two groups. Judging from the few hemoglobin measurements that have been made in wild birds, the hemoglobin content varies from 13 to 16 grams per 100 grams of blood (Dukes and Schwarte, 1932; Nice, Nice, and Kraft, 1935; Groebbels, 1932), and is thus comparable to that in mammals. Nothing is known concerning the comparative blood volumes or the oxygen carrying power of different kinds of hemoglobin. Riddle and Braucher (1934) in extensive blood studies of doves and pigeons, found significant variations in number of blood cells and amount of hemoglobin correlated with age, sex, season, and genetic strain. The blood pressure in birds is apparently not greatly different in large and small species (Woodbury and Hamilton, 1937).

There are considerable data on heart size of European species (Clark, 1927; Groebbels, 1932) but none for species listed in Table 4. With a high heart ratio (heart weight per unit of body weight) we might expect a slower rate at rest and a greater increase in circulation with a given increase in rate. The relative heart size varies inversely with body size, furnishing a means (in addition to high heart rate) of increased circulation in small birds. As a group, birds have relatively larger hearts than mammals (Clark, 1927). Strohl (1910) and Hesse (1921) have reported the heart ratio to be greater at high altitudes and in northern climates, but Stieve (1933) and Rensch (1930) have denied this effect. Clark (1927) shows that the habits of some mammals are related to the heart ratio and to the heart rate. He cites the European hare as being an "athletic" animal with a large heart and a slow rate at rest as compared with the European rabbit, a "non-athletic" animal with a smaller heart and faster rate. In birds, on the other hand, such a relation is not indicated by the data in the literature; in fact, the opposite is indicated in some cases. Swallows and swifts, among the strongest flyers, have a heart ratio as low or lower than weak-flying finches of comparable size (Wahby, 1937).

Individual Variation

As indicated by the data accompanying the standard rates given in Table 4, different ages, sexes, times of day and in a few cases different temperatures are involved. All these are factors which may influence the heart rate of individuals of a species, but each needs to be investigated in more detail before definite conclusions can be made. In the house wren there is little difference in heart rate due to age at a temperature near thermal neutrality, since the standard heart rate of nestlings, juveniles, and adults is about 450 per minute (Tables 1 and 4). At other temperatures, however, great differences occur as has been noted. No conclusion can be made concerning the effect of sex in the species listed. Boas and Landauer (1933) found that the heart rate of the female domestic fowl was distinctly higher than that of the male. Time of day seems to be important. The higher standard rates in Table 4 generally being those taken in the daytime (excluding those taken at the low temperature). For instance, the standard rate for two English sparrows in the daytime was 366 per minute as compared with 310 for three birds at night; three song sparrows in daytime averaged 470 as compared with 425 at night. Even though the conditions (i.e., darkness and temperature) were the same, most individuals tend to be more restless and active when measured in the daytime which probably accounts for the higher rates. However, as already pointed out the rate may be low in early morning. Seasonal differences, especially if they reflect differences in rate of metabolism, may be significant in the study of seasonal activities such as migration.

Effect of Movement

Since muscles make up so large a part of the body of vertebrates and require large amounts of oxygen, it is not surprising that movement is the major factor affecting heart rate, and that the quickest responses and highest rates occur during intense exercise. In man (Boas and Goldschmidt, 1932), the pulse quickens within one or two beats after beginning of exercise or even accelerates in anticipation. In strenuous exercise, the maximum is reached after 1-2 minutes. If work is brief, the rate returns to the former level within 1-2 minutes; if heavy, the effect may continue for hours. Considerable difference in response is apparently due to training; in trained athletes, the increase may not be proportionally so great and the return to the former level quicker.

In birds, an anticipatory response has also been noted. In a few instances, the heart rate quickened noticeably before any detectable movement occurred. Ordinarily, however, acceleration does not occur until after the movement begins, but the response is more rapid than in man and a peak rate may be reached in a few seconds. Following a brief movement, the rate decreases rapidly for 4-5 seconds and more gradually for 10-30 seconds when the former level may be reached. With great activity as in flying, the effect, of course, would be greater and persist for a longer period. The amount of acceleration caused by an individual movement depends a great deal on level of rate before movement; if it is high, due to previous activity or excitement, a particular movement may have little effect.

In this respect, there is considerable value in determining the maximum heart rates. To do this, freshly trapped birds were allowed to fly around the room or exercise vigorously in a small cage and the rate taken as soon as the birds could be caught and

placed against the stethoscope-type of pickup. Maximum rates thus obtained are given in Table 5. It is probable that the absolute peak was not always obtained by the method used as the rate may drop even during the few seconds necessary to get the bird into a recording position. An electric method whereby rate could be followed during as well as after activity would be better here. One experiment was performed in this manner with a song sparrow using subcutaneous needle electrodes and an oscillograph. A maximum of 1,020 per minute was obtained. It seems, then, that the upper limit of normal heart frequency is in the neighborhood of 1,000-1,100 per minute in so far as species listed are concerned, and that this high rate is obtained only by the smaller species.

Effect of Feeding

The immediate and often prolonged effect of food on the heart rate in man and mammals is well known and has been considered in detail by Boas and Goldschmidt (1932), Herrick, et al. (1934), and others, although the exact mechanism (i.e., the specific dynamic action) is not entirely understood. That different types of food, the exercise accompanying feeding, and even the temperature of the food are possible factors causing variation in the response is brought out by these authors.

In birds, the general effect of lack of food has been pointed out in the discussion of the standard rate. The following experiment is an example of how food, as well as activity due to hunger, may influence the heart rate. The heart rate of a day-old chick of the common tern (hatched in the laboratory) was taken at a constant temperature of 95° F. at intervals throughout the day. The bird was fed all the fish it would eat several times as indicated.

Time	*Heart Rate Per Minute*	*Remarks*
9:00 A.M.	...	Fed
10:37	358	
10:53	298	
11:15	342	Restless
11:22	290	
11:30	300	
12:02 P.M.	325	
12:04	325	
12:38	325	
12:50	...	Fed
12:56	390	
1:05	400	
1:17	390	
1:30	380	
1:50	370	
2:10	370	Slightly restless
2:42	360	
2:45	360	
3:00	345	
3:25	390	Very restless
3:27	342	
3:28	340	
3:43	360	
4:02	335	
4:05	370	Restless
4:12	328	
4:15	338	Very restless
4:30	...	Fed
4:40	390	
4:45	390	
5:15	406	
5:30	350	
6:00	380	Restless
6:43	345	

Thus, following feeding in this case, the rate definitely and immediately increased but soon began a gradual decrease. After 1 to 2 hours, the bird became hungry and was likely to become restless and vocal, consequently increasing the rate. However, the rate when quiet still continued to decrease.

Since small birds are usually feeding more or less continually during the day, the effect of food would be continually operative. Only at night and possibly during inactive periods in midday would this effect normally be absent.

TABLE 5. Maximum heart rates of adult and juvenile birds (arranged according to weight).

	Number of Individuals	Time of year	Average wt. at time of recording in gms.	Heart rate per min.	
				Av. max. rate 2-5 sec. after exercise	Highest single reading
Mourning dove*	2	Aug.-Sept.	130.5	435	571
Robin†	1	Sept.	75.8	—	500
Cardinal†	1	Sept.	45.8	—	800
Cowbird†	1	July	44.2	—	779
Catbird†	1	Aug.	41.1	—	734
Towhee *and †	6	Aug.-Sept.	40.5	758	810
Fox sparrow*	1	Oct.	36.7	—	720
English sparrow * and †	11	Aug.-Oct.	28.1	685	902
White-throated sparrow*	5	Sept.-Oct.	26.8	874	1000
White-crowned sparrow*	2	Sept.-Oct.	26.0	891	933
Song sparrow * and †	5	Aug.-Sept.	20.6	945	1021
Junco*	4	Oct.-Nov.	18.0	813	832
Chipping sparrow*	2	Aug.	11.0	971	1040
Chickadee*	2	Oct.	10.5	953	1000
Yellow warbler*	1	July	11.4	—	909
Northern yellow-throat†	1	July	9.2	940	1007

*Adult. †Juvenile.

Sleep

Since the standard rates of adult birds were often taken at night when the bird is likely to be sleeping, the possible effect of sleep as such should be considered.

In man, Boas and Goldschmidt (1932) found that the minimum sleeping rate was less than the basal rate taken when the subject was awake but still in bed in the morning. These authors believe that sleep as such has a definite effect, and that the heart rate during sleep is the result of two factors: (1) diminution of general bodily activities, and (2) active increase in vagal activity. Evidence to support the latter contention was the frequnt occurrence of sinus arrhythmia in sleeping individuals which was interpreted as being due to increased vagus action.

With the setup used, it was not always possible to be certain whether the birds were actually sleeping. With more than 20 healthy and freshly trapped individuals whose rates were taken at night, only one showed distinct arrhythmia. Arrhythmia in birds seems to be more associated with very low rates in captive birds or young birds subjected to low temperatures than to be associated with rates during sleep. No arrhythmia was noticed in 4 individuals sleeping on the nest in nature, although here the rate was high at night due to drop in air temperatures. It may be that sleep is less deep in birds than in man.

MENTAL ACTIVITY

Birds are very easily frightened animals but they also get over the excitement quickly as is shown by their frequent return to the banding traps a short while after capture. In all the laboratory work with wild birds, the technic of handling, the procedure of the experiment, and the set-up of the apparatus was designed to eliminate this factor as much as possible by gentle handling, stimulation of natural conditions, and control of disturbances that might frighten the birds during the course of the experiment. The bird, so to speak, was not aware that its heart rate was being taken, although, of course, it was bound to be affected in some manner by any laboratory procedure. Nevertheless, contrary to Clark's statement (1927, page 92), we believe that the standard heart rate is obtainable from wild animals in the laboratory.

EFFECT OF AIR TEMPERATURE

The marked effect on the heart rate of nestling wrens of small changes in air temperature has been shown. In the last analysis, variation in heart rate due to external temperature depends on the efficiency of the temperature control mechanism. Adults and juveniles have a better temperature control and may be expected to be less sensitive to temperature changes. Nevertheless, even in adults, temperature changes within the ranges of a summer day may have a noticeable effect: 3 male chickadees at 90° F., average standard rate, 519/min.; the same 3 individuals at 70° F., average standard rate, 558/min. The great sensitivity of the heart rate to air temperature is also indicated in Figures 13 and 14 for birds under natural conditions.

In the consideration of temperature effects, the duration of the air temperature as well as the length without food is important. A number of experiments have shown that short exposure to a lower temperature may have little effect. When the temperature is changed from 90 to 70° F., for instance, 30 minutes may pass before the heart rate increases appreciably.

EFFECT OF CAPTIVITY ON WILD BIRDS

Confinement seems to have a marked effect on wild animals. Some cannot successfully be kept in captivity for any great length of time even though their nutrition requirements are known and apparently adequately maintained. Others seem to remain healthy but often lose their alertness and general "wild" characteristics. Benedict and Riddle (1929, p. 531) have shown that even in the domesticated ring dove, the amount of confinement has a definite effect on metabolism. Doves kept in one cubic meter cages for 28-35 days had a basal metabolic rate 10.9% lower than the same birds kept in 75 cubic meter cages. Of 15 birds used in these experiments, 12 showed a distinct lowering of metabolic rate due to confinement and 3 showed no difference. The effect was greater in males (14.9%) than in females (7.3%).

Four English sparrows and one starling were used to test the effect of captivity on the heart rate. English sparrows are principally seed-eaters, are very hardy, and "thrive" in captivity as well or better than other small birds. Standard heart rates of the birds were first taken when freshly trapped, following which the birds were placed in an outdoor cage 6 x 8 x 8 feet so that they would be subjected to normal out-of-door conditions and would have considerable space in which to fly around. Abundant food was supplied in the form of mixed grains (cracked corn, buckwheat, and sunflower seed) and loaf bread; water was available at all times. After four days to three weeks, the birds were removed from the cage at the same time of day as their original capture and standard heart rates taken with identical procedure and conditions. All the experiments were run in June and July, and none of the birds had ever been captured previous to the experiments.

Four out of five birds (Table 6) had a distinctly lower standard heart rate after caging, while the fifth bird, a female, was not affected as its heart rate was slightly higher after 10 days in captivity. The effect thus varied from 0 to 34%, the average for all five birds being a 19.0% decrease in heart rate. This decrease was not necessarily accompanied by a loss in weight as in two out of three English sparrows showing a captivity effect the weight remained virtually the same and in the third case, it decreased only 6%. Since weight is a reliable indicator of physiological condition, it would appear that the lowering of the heart rate is not the result, entirely at least, of malnutrition, and that the birds were maintained in good condition. That the effect may occur in a very short time is indicated by the case of the starling (Table 6).

In addition to the decrease in rate, a striking result was the appearance of a very irregular beat or sinus arrhythmia in three out of five cases. Arrhythmia here consisted of alternating very slow, irregular beats and more rapid, regular beats (Fig. 1E). The standard rate shown in Table 6 is the net rate including both slow and fast sections. No arrhythmia whatever was noted in the birds when first trapped. When birds showing arrhythmia were removed from the temperature chamber after the experiment and held to the ear, the heart beat was perfectly regular, showing that the irregular rhythm was definitely as-

sociated with the low standard rate. Arrhythmia, as already pointed out, is often normally present in sleeping human beings; it was observed in cold-blooded nestlings at low temperatures, and in a few freshly trapped adults at the low standard rate. It would seem, then, that when the heart rate becomes very low, irregular rhythm may appear. No particular detrimental effect seems to result as birds exhibiting arrhythmia have lived for weeks after its occurrence was noted.

This marked arrhythmia might be considered as an exaggerated form of the "oscillatory fluctuations" in heart rate that normally occur. If it is assumed that periodicity in vagus action causes the oscillations, increased vagus action might well result in such a rhythm as shown in Figure 1E.

From the above evidence on heart rate and metabolism, it seems likely that the loss of wildness in birds and general decline in vigor so often produced by confinement is accompanied by a decrease in rate of metabolism which may be a result of the curtailment of their activity and the interruption of normal rhythms of behavior.

TABLE 6. Effect of captivity on heart rate.

Species	Individual	Freshly Trapped: Age and sex	Weight gms.	Standard rate per min.	After Confinement In Outdoor Cage: Days captive	Weight gms.	Standard rate per min.
English sparrow	37–2	Adult Male	28.0	303	12	26.4	243
English sparrow	37–4	Adult Female	29.9	378	10	—	389
English sparrow	38–2	Adult Male	31.0	305	18	30.8	245*
English sparrow	38–3	Juvenile	29.4	323	14	30.3	236*
Starling	No. 4	Adult	—	340	4	—	223*

*Marked arrhythmia.

There is also evidence to indicate that permanent confinement and especially domestication of birds may result in permanent morphological and physiological changes. Gerstell and Long (1939) have found that the rate of metabolism in tame strains of the turkey was lower than in wild strains. The heart ratio is apparently much less in the domestic fowl than in comparable wild species; from Hesse's (1921) data, we get:

	Body Wt. in Gms.	*Heart Wt. Per 1000 Gms. Body Wt.*
Domestic fowl	2000-3000	4.0-4.6
Capercaillzie (wild grouse)	4000	9.1
Blackcock (wild grouse)	1300	11.0

Buchanan (1909) gives the heart ratio of the canary as 10.4 compared with 13 to 15 for small wild finches. Dukes and Schwarte (1931) have shown that wild gallinaceous birds have 13.7 to 14.9 grams of hemoglobin per 100 grams of blood as compared with 9.8 grams in the domestic fowl. In general, these data would indicate that domestic birds are physiologically inferior to comparable wild species. Hence, it may not be entirely correct to speak of the condition in "birds" when data are concerned only with domestic species.

HEART RATE OF BIRDS IN NATURE

One of the principal purposes in the development of the vibrometer was to use it directly in the field, so that the heart rate of birds under natural conditions could be determined and comparisons made with the results obtained under controlled conditions in the laboratory. Records of heart rate of birds on the nest were first obtained during the summer of 1938. While the results from these measurements must be considered preliminary, they indicate some of the possibilities of the apparatus for field use and represent the first records of heart beat obtained with wild birds in an entirely free and natural condition.

METHODS

With an open nest, such as that of the catbird, the crystal was mounted on a small platform next to the nest (Plate I, Fig. 17). A shallow wire basket was slipped under the nest and attached to the perch. Variations in pressure on the nest were thus brought to bear on the crystal. When a bird sat on the eggs, the heart beat produced enough force to vibrate nest and all. For use with species that nest in boxes, as in the case of the house wren, the wire platform under the nest was extended through a small hole in the box and attached to the perch crystal located outside (Fig. 18). In both cases, there was little disturbance of the actual nest. The amplifier and recorder were operated from a blind near the nest (Fig. 22). The house current necessary to operate the amplifier and recorder was obtained through the use of a long extension cord.

The equipment at the nest was set up gradually so as to disturb the normal behavior of the birds as little as possible. The platform and the blind were put up first and a day or so allowed for the birds to become used to them. Then the crystal was put in place, camouflaged with leaves, and the other units placed in the blind. Each of these operations required only 5-10 minutes. Recording was not started until several hours after final adjustments were made. There is no reason to believe that the normal behavior of the birds was materially changed. The air temperature was measured by means of a mercury thermometer accurate to 0.1° F. placed either close to the nest or in a similar location as regards exposure.

NORMAL DAILY VARIATION IN THE HEART RATE OF INCUBATING BIRDS

Records over 24 hours were obtained of two female house wrens and one female catbird; records during

the daytime were obtained for another female catbird. In both these species, only the female incubates.

Figure 12 shows the variations, including oscillatory fluctuations and the general trend, in the heart rate which occur during a typical attentive period in the middle of the day; that is, the heart rate from

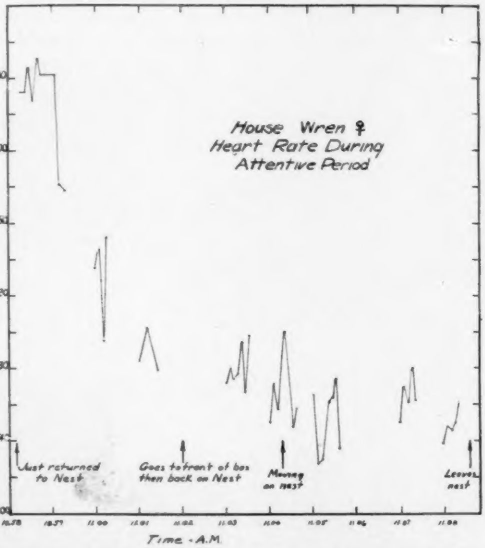

FIG. 12. The heart rate of a female house wren during a typical attentive period on the nest as indicated by readings every one to two minutes. Both the oscillatory fluctuations and general trend are indicated.

the time the bird arrives on the nest following an inattentive period (when it has been flying around and feeding) to the time it leaves the nest again. Periodic behavior during incubation is characteristic of many small birds. In the house wren, the attentive periods average 10-15 minutes; the inattentive periods, 5-10 minutes, but there are wide variations. The attentive periods average about 24 minutes in the catbird. The average variation in the heart rate of a female house wren during attentive periods in

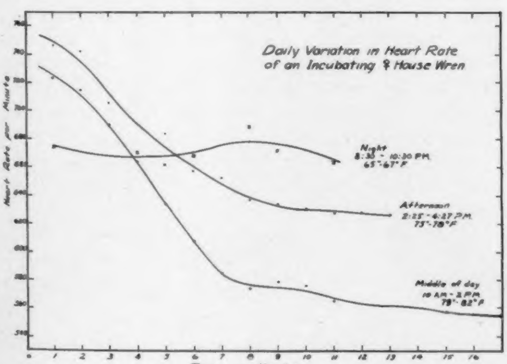

FIG. 13. The heart rate of an incubating female house wren at different times of day. See text for explanation.

the afternoon, night, and morning together with the air temperatures are shown in Figure 13. Each daytime curve is an average of several attentive periods while the night-time curve is based on a number of recording periods of comparable length. Similar averages for a female catbird are plotted in Figure 14. Although these figures are based only on single individuals, the data of the other individuals agree very closely.

During the daytime attentive period, the heart rate falls rather rapidly during the first 8 to 9 minutes on the nest and then more gradually until the bird leaves the nest. This trend of rate takes place even though the bird may move around on the eggs at intervals or even get off the nest for a few seconds (Fig. 12); these movements usually cause only momentary increases in heart rate. A rather consistent difference occurred between the house wren and the catbird which seemed to be related to differences in behavior while on the nest. In both catbirds, the greatest drop in rate occurred during the first three minutes or less after the bird arrived on

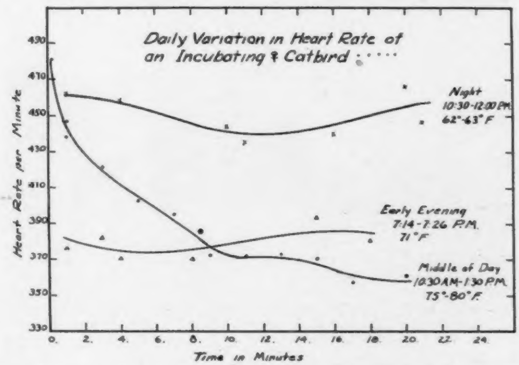

FIG. 14. The heart rate of an incubating female catbird at different times of day. See text for explanation.

the nest, whereas in the house wren, a delay of about two minutes occurred before the rate dropped materially. Thus, the curves are respectively "concave" and "convex." The catbird on arriving on the nest usually settled down on the eggs rather quickly and remained fairly quiet; the wren, on the other hand, was much more fidgety and tended to spend a longer time in settling down.

The difference in heart rate during the day and during the night was marked (Figs. 13, 14). During the day, the heart rate was high while the bird was active. It probably varied between 700 and 1,000 per minute in the house wren judging from maximum rates known and from the rate when the bird first arrived on the nest, and between 500 and 750 per minute in the catbird. After the birds had been on the nest for a few minutes, the rate fell to 550-650 in the house wren and 320-390 in the catbird. At night, on the other hand, the bird was continually on the nest and the average rate remained more or less constant at a level significantly higher

than the resting level during the daytime, or approximately 670 per minute for house wren and 460 per minute for the catbird. That this high level may be maintained during the later part of the night as well as around midnight is shown by a record made at 3:00 A.M. (not shown in graphs) at which time the rate of a female house wren averaged 701 per minute.

It appears, then, that the average rate was greater in the daytime due to greater activity and fluctuated widely, but the resting rate was greater at night than in the day. This would seem to be correlated with temperature, which was lower at night. Muscle tremors were noticeably greater at night (when temperatures were 60-70° F.) than during the day (when temperatures were 75-90° F.). Tremors were periodic in occurrence and intensity as has been observed in the laboratory. In addition to an increase in tremors, actual movements were greater at night than when the bird was incubating during the daytime. All three birds studied at night were decidedly "restless" on the nest, moving at short intervals. Usually these movements were of short duration involving changes in position but more pronounced movements often occurred. The catbird often hopped up on the edge of the nest and back again, and the wrens often got off the nest entirely and went up to the front of the box. It was very noticeable that when tremors decreased or stopped, a pronounced movement usually followed. It would seem that the combined action of tremors and movements is ample to explain the high heart rate at night at low temperatures, the tremors acting more or less continuously and the movements at intervals.

This daily rhythm of heart rate is apparently just the opposite of the typical daily rhythm in body temperature. The body temperature of both house wrens and catbirds as well as other species while incubating is 2-3 degrees higher when the bird is quiet on the nest in the daytime than at night

PLATE I.

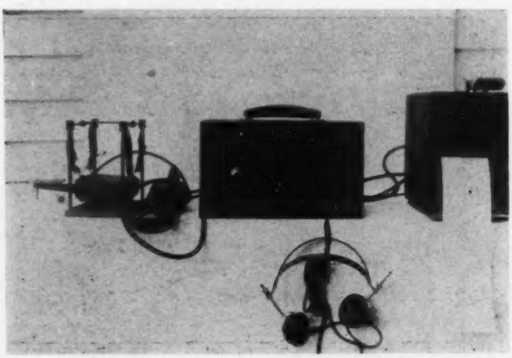

FIG. 15. The three units of the cardio-vibrometer, from left to right: the pickup or perch crystal, the amplifier, the pen recorder.

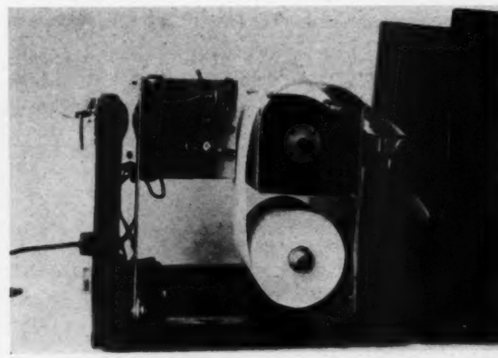

FIG. 16. View of the pen recorder from the side showing details of construction. Note metal case enclosing crystal, ink well, pen, synchronous motor, paper and paper drive.

FIG. 17. An incubating catbird having its heart rate measured. The nest is resting in a wire basket attached to the pickup crystal arm. This is an entirely wild bird on its natural nest.

FIG. 18. The perch crystal set up at a wren box. The sensitive arm extends into the box through a small hole in the back so as to rest just under the nest. The bird enters through the regular entrance in the front of the box.

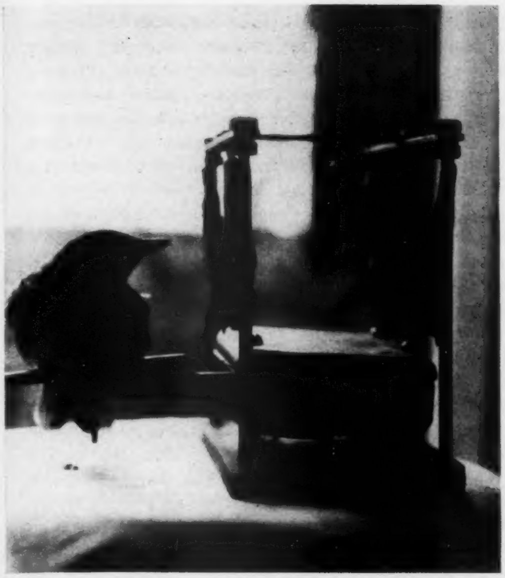

FIG. 19. A juvenile robin sitting on the perch crystal in the best position for recording the heart beat, breathing, tremors, etc.

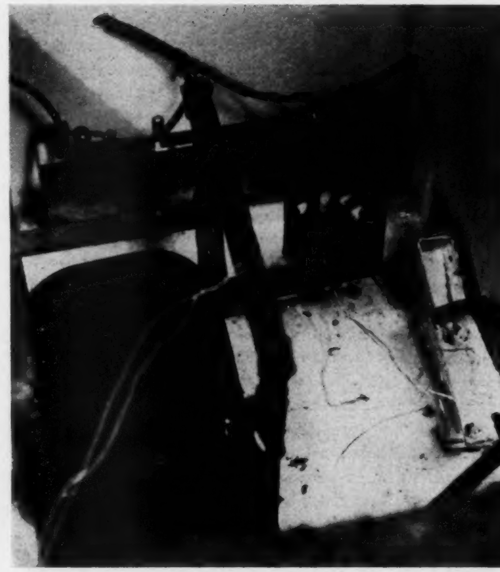

FIG. 21. Interior view of the temperature chamber, showing method of recording the heart rate of nestlings. The nestling can be seen inside the small box attached to the crystal arm. One of the two heaters and the thermocouples are shown.

FIG. 20. Temperature chamber with thermoregulator in the top. The device to the extreme right is the stethoscope type of pickup. The white wires are thermocouple leads.

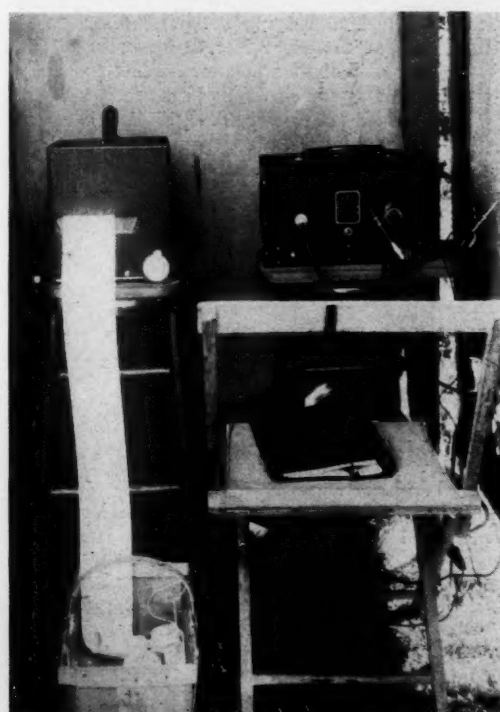

FIG. 22. The amplifier and recorder units set up in a blind near the nest for use in field recording.

(Baldwin and Kendeigh, 1932). Since body temperature was measured by means of thermocouples placed in the nest, the results should be quite comparable with results obtained in measurement of heart rate.

The standard rate of the house wren as determined in the laboratory under a constant temperature of 92° F. is about 450 per minute (see Table 6). A rate this low is apparently rarely, if ever, obtained in nature. The tendency for the rate to decrease at night when no food is taken is more than counteracted by the increase due to tremors and activity accompanying lower temperatures. The temperature at night would presumably have to be 92° F. before a rate of 450 per minute was obtained in nature. In contrast, a standard body temperature of 104° F. (40.0° C.) is commonly reached at night, or the body temperature may even go slightly below it.

Some study was made of breathing rates which accompanied heart rates under different conditions on the nest. Breathing rate in the house wren was between 160 and 200 per minute as the bird arrived on the nest during a daytime attentive period and dropped to about 100 per minute after 10 minutes. The average at night was 102 per minute. The average standard respiration rate of four individual house wrens in the laboratory was 75 per minute.

GENERAL DISCUSSION

The main idea underlying the present study has been the use of the heart rate as an index to the physiological state of the whole animal and especially as an indicator of the changes which take place due to different conditions under which the animal lives. The measurement of many functions requires equipment and procedures which can often be used only under rather limited circumstances in the laboratory, and while such experimentation is very important in determining physiological mechanisms, it is not always applicable to wild animals or to conditions in nature. The heart rate as measured by the vibrometer would seem to provide a means of studying the physiological responses of wild animals under less disturbed laboratory conditions and also under actual conditions in nature.

We have seen that the heart rate in small birds is a very sensitive index not only being inherently variable but changing rapidly in response to many activities and stimuli. The determination of a standard rate or some stabilized rate is, therefore, necessary in order to compare species as well as to provide a convenient basis for the evaluating of the effects of various factors. Likewise, variability emphasizes the need for quantitative data. Frequent recordings and the random sample method of analysis were adopted in an attempt to obtain adequate data, but even so, the results were often fragmentary. It is hoped that eventually a method of continuous recording can be applied to the piezo-electric system. The standard rate does not seem to remain constant for a very long time in small birds. Consequently, it is important to define the time limits rather closely if the results are to be comparable. While five or six hours might not make much difference in man or larger animals, it may make a considerable difference in small birds. The evidence indicates that the various factors concerned in daily rhythms are important in standard rate determination. This phase is a promising one for further study.

A close correlation between the heart rate and the metabolic rate has been suggested by many investigators. The circulatory system is one of the most responsive systems in the vertebrate body since it must supply the changing demands for food, oxygen, and waste removal, the sum total of which constitutes the metabolism of the entire organism. Variation in the heart rate is the most important means, although not the entire one of bringing about many of the changes in circulation. Variations in blood pressure, output of the heart per beat, amount of oxygen and food available in the blood are all factors playing a part in the adjustments of the organism, but for practical purposes, the heart rate seems to be proportional to the circulation rate. Henderson (1923) in a review on the volume changes of the heart, states: "The stroke volume in the normal man or animal is practically a uniform quantity (within 20-30%) during all the ordinary activities of life. The circulation rate is, therefore, nearly proportional to the pulse rate." More recently, Herrick, Essex, Mann, and Baldes (1934) made accurate measurements of blood flow by means of thermocouples on the intact animal and showed a very close correlation between circulation rate and pulse rate in dogs. However, in actual practice in dealing with animals, it is often found that while measurements of metabolism are approximately correlated with the heart rate, there are often discrepancies. At least two good reasons can be advanced: (1) Metabolism measurements as they are usually made are averages often over long periods of time, while heart rate measurements are usually only brief samples. To be truly comparable, metabolism measurements should be made from minute to minute, or conversely, heart rate averaged over longer intervals. (2) The strong inervation of the heart and the great influence of the conscious centers introduces fluctuations, often transitory, which possibly may not be accompanied by corresponding appreciable increases in heat production although this has not been studied. As already suggested, variations in blood composition, etc., may affect the heart rate-metabolism relationship, especially where species are compared or individuals at different times and ages. However, comparative information on this subject is very small.

Rate of metabolism and heart rate as they vary with air temperature in nestling house wrens are very closely correlated, which indicates that heart rate is a reliable index to metabolism, at least in so far as temperature effects are concerned. If further studies extend the relation to include factors other than temperature, it would then be possible to calculate the

rate of metabolism from the heart rate obtained in nature, for instance, where it is not now possible to measure gaseous exchange or heat production directly.

Muscle tremors at lower air temperatures seem to be proportional to the heart rate and metabolic rate, and from the quantitative measurement of tremors considerable can be learned. On the other hand, body temperature may not always be directly related to heart rate, since heart rate (and presumably rate of metabolism) seems to increase at night with the drop in air temperature while the body temperature decreases. Decreasing body temperature also accompanies increasing heart rate in 6-day nestlings when the air temperature drops from 100 to 90° F. A similar relation may possibly also occur with extended starvation. Likewise, the relation of rate of breathing and heart rate may be different under different conditions. It is directly correlated with heart rate in nestlings at air temperatures of 70 to 100° F., but at 105° F., it increases to a much greater extent. Thus, the point of sharp increase in breathing rate at high temperatures indicates a critical point in the functioning of the heat loss mechanism.

In short, the heart rate is related to other physiology-of-the-whole measurements (e.g., rate of CO_2 production, muscle tremors, body temperature, and breathing rate) in different ways, and the relations may vary with age and environmental conditions. Therefore, it is important to know the relation of the heart rate to other physiological variables in order to better understand the response of the organism to the conditions under question.

Confinement of wild birds even for a few days seems to have a marked effect; the heart rate is decreased and the evidence strongly suggests that heat production is also decreased. Therefore, if the wild condition is to be measured, birds must not be kept captive any longer than necessary. The captivity effect also suggests that perhaps a wide range of activity is important in maintaining a high functional level. Supporting such a contention is the evidence which indicates that such relatively inactive domestic birds as the domestic fowl and canary are physiologically inferior to comparable wild species.

The marked sensitivity of the circulatory system to changes in environmental temperature is demonstrated both in the laboratory and field measurements. The degree of response seems to be greatest in nestlings, but even a change in air temperature of 15° F. such as commonly occurs between day and night has a marked effect on the heart rate of adults. The field results are here especially interesting as they show that low temperature at night puts a considerable strain on the circulatory system and the temperature regulation, which means that a large amount of food energy must be taken during the day and a reserve built up over and above the need for daytime activities for use at night. This great physiological sensitivity is closely related to the behavior of the birds. Physiological responses to a change in temperature or other conditions are often accompanied by behavior responses. Thus, the great activity of birds during the cool part of the day and their restlessness on the nest at night is explained, to cite but two examples. Behavior regulation (seeking shelter, food) reduces but does not remove the strain on functional regulation (increased heart rate, metabolism, etc.). Consequently, in addition to food and shelter requirements, the degree of physiological change which is necessary to meet climatic conditions is important in determining the limits of tolerance and, consequently, in limiting the distribution of the species. The data so far obtained indicate that measurement of the heart rate (together with breathing rate and muscle tremors) is a means of determining the physiological sensitivity of different individuals, ages and species to environmental conditions.

SUMMARY

1. A new apparatus, the cardio-vibrometer, is described which utilizes the piezo-electric principle and has the following advantages: (1) Records can be made with a minimum of disturbance to the animal and under a variety of experimental and natural conditions. (2) Records are immediately available and quantitative recording facilitated. (3) It is portable, comparatively rugged yet very sensitive, and requires a minimum of adjustments. (4) Breathing, muscle tremors, and general activity can be recorded in addition to heart beat. The graphic records or cardio-vibrograms are neither electrocardiograms nor heart sound records; they are variable in form, but are adapted to the accurate calculation of heart rate.

2. The heart rate of small birds varies considerably from moment to moment in a distinctly oscillatory manner. Oscillations are never very regular and occur from 3-15 times per minute. These fluctuations which may amount to as much as 18% of the average rate during a single minute appear to be physiologically inherent and are not associated with events in the breathing cycle. In addition, smaller and very transitory fluctuations sometimes but not always occur with each breathing cycle.

3. The standard rate is defined as the heart rate of the bird in a post-absorptive but not starved condition, in darkness, away from human presence, and at any specified temperature. For comparisons between species, thermal neutrality seems best. In small passerine birds (less than 100 gms. in weight) the standard rate may be obtained approximately 3 hours after capture, but is preferably taken during the interval 4-7 hours after capture. The standard rate is not maintained constant for very long; it tends to decrease gradually as the period without food continues. Long starvation may result in increased activity and a more variable heart rate. In mourning doves at least 14 hours of starvation should be allowed and preferably 18 to 24 hours.

4. Standard heart rates of 6 ages of nestling house wrens (0 to 15 days old) were determined at 6 temperatures (70 to 105° F. or 21.1 to 40.6° C.). The standard heart rate varies directly with air temperature in 0- and 3-day nestlings, and varies inversely with air temperature in 12- and 15-day nestlings;

intermediate relations occur at 6 and 9 days of age. These changes are related to the development of the temperature control mechanism. The point of lowest heart rate or zone of thermal neutrality in the warm-blooded nestlings (9, 12 and 15 days old) is approximately 100° F.

5. Heart rate varies with air temperature in a very similar manner as does the rate of metabolism as indicated by CO_2 production, showing that heart rate is a reliable index to the rate of metabolism, at least in so far as temperature effects are concerned.

6. Heart rate increases with increasing age at low temperatures (70 and 80° F.), but is approximately the same for all ages at higher temperatures (100 and 105° F.). Rate of metabolism (CO_2 production), on the other hand, increases significantly with age at higher temperatures. This difference probably can be explained by changes in the erythrocyte number and hemoglobin content of the blood which are reported to occur during the nest life of altricial species.

7. A markedly irregular beat, or sinus arrhythmia, is often associated with low heart rates of 0- and 3-day nestlings at an air temperature of 70° F. Arrhythmia also may accompany a decrease in standard rate due to captivity (see No. 13) and was observed in a few freshly trapped adults under standard conditions. Two types of arrhythmia are illustrated. One consists of series of slow irregular beats alternating with rapid regular ones; in the other each beat is alternately rapid and prolonged.

8. No muscle tremors are detectable at 0 and 3 days of age, but are present at all greater ages. Duration and frequency varies directly with heart rate and inversely with air temperature. Tremors are periodic at the higher temperatures and become more continuous as the temperature decreases, although the frequency and intensity may continue to vary periodically. Tremors immediately accompany an increase in heart rate, and are undoubtedly an important factor in causing an increase in the standard heart rate and metabolism with a drop in temperature. Tremors are less frequent in adult and juvenile than in nestling birds at comparable temperatures, and the heart rate correspondingly increases less with a drop in temperature.

9. Rate of breathing varies with temperature as does the heart rate, but increases at 105° F. to a much greater extent. This is associated with a marked increase in water loss, and indicates the importance of the breathing rate in heat loss in birds.

10. Standard heart rates, mostly at thermal neutrality, of 39 individual adult and juvenile birds of 14 species were determined. Generally speaking, the standard rate is inversely proportional to body size, but where small differences in size are concerned, the correlation is not consistent. Relative heart size, age, sex, time of day and year, blood composition, and life habits are suggested as possible factors affecting the comparative heart rates of species and individuals.

11. The standard rate was generally higher in daytime than when measured at night under same conditions of darkness and temperature, although in the early morning (before bird has recovered weight lost during the night) the rate may be low. More data are needed to clarify factors involved in daily variations.

12. Maximum heart rates of 16 species taken following strenuous exercise are listed; in 6 of the smallest species a rate of 1,000 per minute or over has been recorded. Increase in heart rate as a result of muscular activity is very rapid. Acceleration in anticipation to movement has been noted in some cases, both in the laboratory and in the field.

13. Food and mental activity have important effects on the heart rate of birds; these factors must be controlled in order to judge the effect of other factors.

14. English sparrows and starlings confined to outdoor cages and well supplied with food and water had an average decrease of 19% in the standard heart rate after 4-20 days, although their weight did not decrease in 2 out of 3 cases in which it was measured. It is suggested that captivity may have permanent effects on the circulatory system and that domestic birds may be physiologically inferior to comparable wild species.

15. The heart rate of two species (house wren and catbird) in nature was obtained by inserting the crystal under the nest and operating the recording instruments from a blind. During a daytime attentive period on the nest, the heart rate of the incubating female decreases rather rapidly during the first 8 minutes after the bird arrives on the nest, then decreases very gradually until she leaves the nest. This drop was approximately from 740 to 600 per minute in the house wren and from 480 to 375 per minute in the catbird when the air temperature was approximately 80° F.

16. The heart rate of the incubating bird on the nest at night was distinctly higher than when the same bird was resting quietly on the nest in the daytime. This is correlated with the drop in air temperature and the increase in muscle tremors and general activity on the nest which occurred at night. In the house wren, the increase in heart rate at night amounted to 18%, accompanying a drop in temperature of 15° F. from 81 to 66° F.; in the catbird, a 26% increase occurred accompanied by a drop of 15° F. in air temperature from 77.5 to 62.5° F. The daily rhythm in heart rate may thus be opposite from the daily rhythm in body temperature. Consequently, even with a decrease in body temperature there is a considerable strain on the circulatory and temperature regulatory systems at night.

17. The extreme variation of heart rate of incubating house wrens in nature during a 24-hour period (temperature 65-85° F.) was 540 to 805 per minute compared with 450 per minute, the average standard rate at 92° F. of same species in the laboratory. Apparently a rate as low as 450 is rarely if ever obtained in nature since the tendency for the rate to decrease at night when no food is taken and the bird remains on the nest is counteracted by the decrease in temperature. Likewise, the breathing rate varied from 100 to 200 per minute in nature as compared

with an average standard rate of 75 per minute under constant conditions in the laboratory.

18. The data so far obtained indicate that measurement of the heart rate (together with breathing rate and muscle tremors) with the cardio-vibrometer is a means of determining the physiological response and sensitivity of different individuals, ages and species to environmental conditions.

APPENDIX

SCIENTIFIC NAMES OF THE BIRDS MENTIONED IN THIS STUDY

For North American species, the nomenclature of the American Ornithologists' Union Check-List, Fourth Edition, 1931, is followed, except that subspecific names are omitted.

North American Species

Common Tern, *Sterna hirundo* Linnaeus.
Mourning Dove, *Zenaidura macroura* (Linnaeus).
Ruby-throated Hummingbird, *Archilochus colubris* (Linnaeus).
Black-capped Chickadee, *Penthestes atricapillus* (Linnaeus).
House Wren, *Troglodytes aedon* Vieillot.
Catbird, *Dumatella carolinensis* (Linnaeus).
Brown Thrasher, *Toxostoma rufum* (Linnaeus).
Robin, *Turdus migratorius* Linnaeus.
Starling, *Sturnus vulgaris* Linnaeus.
Yellow Warbler, *Dendroica aestiva* (Gmelin).
Northern Yellow-throat, *Geothlypis trichas* (Swainson).
English Sparrow, *Passer domesticus* (Linnaeus).
Cowbird, *Molothrus ater* (Boddaert).
Cardinal, *Richmondena cardinalis* (Linnaeus).
Towhee, *Pipilo erythrophthalmus* (Linnaeus).
Slate-colored Junco, *Junco hyemalis* (Linnaeus).
Chipping Sparrow, *Spizella passerina* (Bechstein).
Field Sparrow, *Spizella pusilla* (Wilson).
White-crowned Sparrow, *Zonotrichia leucophrys* (Forster).
White-throated Sparrow, *Zonotrichia albicollis* (Gmelin).
Fox Sparrow, *Passerella iliaca* (Merrem).
Song Sparrow, *Melospiza melodia* (Linnaeus).

European Species

Capercaillzie, *Tetrao urogallus* Linnaeus.
Blackcock, *Lyrurus tetrix* (Linnaeus).
European Goldfinch, *Carduelis carduelis* (Linnaeus).
Greenfinch, *Chloris chloris* (Linnaeus).

Domestic Species

Domestic Fowl, *Gallus domesticus*.
Domestic Pigeon, *Columba livia*.
Ring Dove, *Streptopelia risoria*.
Canary, *Serinus canarius*.

LITERATURE CITED

Anrep, Pascual, and Rössler. 1936. Proc. Roy. Soc. **119B**: 191 (quoted in Starling, Human Physiology, 7th edition).

Baldwin, S. Prentiss, and S. Charles Kendeigh. 1932. Physiology of the temperature of birds. Sci. Pub. Cleveland Mus. Nat. Hist. **3**: 1-196.

——— 1938. Variations in the weight of birds. The Auk **55**: 416-466.

Barcroft, J., and J. J. Izguierdo. 1931. The relation of temperature to the pulse rate of the frog. Jour. Physiol. **71**: 145-155.

Barott, H. G., J. C. Fritz, E. M. Pringle, and H. W. Titus. 1938. Heat production and gaseous metabolism of young male chickens. Jour. Nutrition **15**: 145-167.

Bartsch, Paul, W. H. Ball, W. Rosenzweig, and S. Salman. 1937. Size of red blood corpuscles and their nucleus in 50 American birds. The Auk **54**: 516-519.

Benedict, F. G., and Oscar Riddle. 1929. The measurement of basal heat production of pigeons. Jour. Nutrition **1**: 475-536.

Boas, E. P., and E. F. Goldschmidt. 1932. The heart rate. Springfield, Ill., 132 pp.

Boas, E. P., and Walter Landauer. 1933. The effect of elevated metabolism on the hearts of the frizzle fowl. Amer. Jour. Med. Sci. **185**: 654-664.

Bogue, J. Yule. 1932. The heart rate of the developing chick. Brit. Jour. Exp. Biol. **9**: 351-358.

Boulton, Rudyerd. 1927. Ptilosis of the house wren. *(Troglodytes aedon aedon)*. The Auk **44**: 387-414.

Buchanan, Florence. 1909. On the frequency of the heart beat in birds. Jour. Physiol. **39**, Proc. xxv.

——— 1910. The significance of the pulse rate in vertebrate animals. Annual Report, Smithsonian Inst. 487-505.

Clark, A. J. 1927. Comparative physiology of the heart.

Dukes, H. H., and L. H. Schwarte. 1931. The hemoglobin content of the blood of fowls. Amer. Jour. Physiol. **96**: 89-93.

Fleisch, A. 1930. Schweiz. Med. Wschr. **62**: 254. (Quoted in Starling, Human Physiology, 7th edition.)

Gerstell, Richard, and W. H. Long. 1939. Physiological variations in wild turkeys and their significance in management. Res. Bull. No. 2, Penn. Game Com., 57 pp.

Groebbels, F. 1932. Der Vogel. **1**: Berlin, 918 pp.

Gulliver, G. 1876. Observations on the sizes and shapes of red blood corpuscles of the blood of vertebrates. Proc. Zool. Soc. London. 474-495.

Henderson, Y. 1923. Volume changes of the heart. Physiol. Rev. **3**: 165-205.

Herrick, J. F., H. E. Essex, F. C. Mann., and E. J. Baldes. 1934. The effect of digestion on the blood flow in certain blood vessels of the dog. Amer. Jour. Physiol. **108**: 621-628.

Hesse, R. 1921. Das Herzgewicht der Wirbeltiere. Zool. Jahrb. **38**: 243-364.

Kalabukhov, N., and V. Rodinov. 1934. Changes in the blood of animals according to age. Folia Haematologica **52**: 145-158.

Kendeigh, S. Charles. 1934. The role of the environment in the life of birds. Ecol. Monogr. **4**: 299-417.

——— 1939. The relation of metabolism to the development of temperature regulation in birds. J. Exp. Zool. **82**: 419-438.

Koppanyi, T., and M. S. Dooley. 1928. The cause of cardiac slowing accompanying apnea in the duck. Amer. Jour. Physiol. **85**: 311-323.

Laurens, H. 1914. The influence of temperature on the rate of heart beat in Amblystoma embryos. Amer. Jour. Physiol. **35**: 199-210.

Mitchell, H. H., L. E. Card, and T. C. Hamilton. 1932. A technical study of the growth of white leghorn chickens. Univ. of Ill. Ag. Exp. Sta. Bull. 367.

Nice, L. B., M. M. Nice, and R. M. Kraft. 1935. Erythrocytes and hemoglobin in the blood of some American birds. Wilson Bulletin **47:** 120-124.

Odum, Eugene P., and S. C. Kendeigh. 1940. The cardio-vibrometer: A new instrument for measuring the heart rate and other body activities of animals. Ecology **21:** 105-106.

Riddle, Smith C., and F. G. Benedict. 1932. The basal metabolism of the mourning dove and some of its hybrids. Amer. Jour. Physiol. **101:** 260-267.

Riddle, Oscar, and P. F. Braucher. 1934. Hemoglobin and erythrocyte differences according to sex and season in doves and pigeons. Amer. Jour. Physiol. **108:** 554-566.

Romanoff, A., and M. Sochen. 1936. Thermal effects on the rate and duration of the embryonic heart beat of *Gallus domesticus*. Anat. Rec. **65:** 59-68.

Shelford, Victor E. 1929. Laboratory and Field Ecology. Baltimore, 751 pp.

Starling, E. H. 1936. Human Physiology, 7th Ed. Philadelphia,

Stevenson, James. 1933. Experiments on the digestion of food by birds. Wilson Bull. **45:** 155-167.

Stieve, H. 1933. Untersuchungen an Wirbeltierherzen. 1. Der Einfluss des Aufenthaltes in hohen Lagen auf die Herzgrösse einiger Vogelarten. Zool. Anz. **101:** 233-246.

Stresemann, Erwin. 1934. Aves. Kukenthals' Handbuch der Zoologie, Bd. 7. 899 pp.

Strohl, J. 1910. Uber Herzverhältnisse bei nächstverwandten Vogelarten aus den Hochalpen und der Lappländischen Ebene. Zentralblatt d. Physiol. **24:** 38-103.

Stubel, H. 1910. Beiträge zur Kenntnis der Physiologie des Blutkreislaufs bei verschiedenen Vogelarten. Pflügers Archiv für gesamte Physiol. **135:** 249-365.

Wahby, A. 1937. Recherches sur les poids du cœur, de l'encephale et du gesier par rapport à celui du corps chez les oiseaux. Alauda **9:** 143-250. (Review in Auk **55:** 310.)

Woodbury, R. A., and W. F. Hamilton. 1937. Blood pressure studies in small animals. Amer. Jour. Physiol. **119:** 663.

ROOT HABITS OF CERTAIN PLANTS OF THE FOOTHILL AND ALPINE BELTS OF ROCKY MOUNTAIN NATIONAL PARK

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ROOT HABITS OF CERTAIN PLANTS OF THE FOOTHILL AND ALPINE BELTS OF ROCKY MOUNTAIN NATIONAL PARK

INTRODUCTION

This study includes: (1) an investigation of environmental differences which affect plant growth in the foothill, montane, and alpine belts of Rocky Mountain National Park; and (2) a detailed study of the underground habits of 30 representative species of the foothills and 34 species of the alpine belt.

Rocky Mountain National Park of Colorado, like other areas in the Rocky Mountains, may conveniently be divided into four climatic or life belts: foothill, elevation between 6,000 and 8,000 ft.; montane, 8,000 to 10,000 ft.; subalpine, 10,000 ft. to timberline (11,000 to 11,500 ft.); and alpine, above timberline. Although there is much overlapping of the floras, especially of adjacent belts, the vegetation of each belt is distinctive enough to be recognizable readily without resorting to a detailed analysis.

The exact measurement of environmental factors affecting plant growth in the Rocky Mountain region has been undertaken in but few instances. From extensive studies in the Pike's Peak area Whitfield (1933) concludes that both day and night temperatures, soil temperatures, and moisture saturation deficit, decrease with an increase in altitude. Whitfield (1932, 1933) concludes that transpiration and growth decrease with an increase in altitude. Sperry (1936) found that water loss from atmometers and water transpired from cut twigs of trees decreased progressively from the foothills to the subalpine belt. This is in agreement with results of the phytometer studies of Clements and Goldsmith (1924) and of Clements, Long, and Martin (1937, 1938). The latter authors have demonstrated that the water requirement of plants decreases with increases in altitude from plains to the alpine belt. Shreve (1924) determined that increases of altitude are associated with decreases of soil temperature.

Previous studies of mountain plants have not been concerned primarily with the underground parts. Schimper (1903) states that the desiccating action of the mountain climate results in a strong development of roots (especially in the alpine belt) characteristic of xerophytes. Warming (1909) and Holm (1927) have published incomplete drawings of underground systems of numerous alpine and other mountain plants.

Whitfield (1933) has described the several rows of palisade and the larger number of stomatal openings on the upper surface of the leaves of alpine plants. This is in agreement with Warming (1909), who believed that alpine plants are vigorous in "assimilation" because of their better developed palisade. Ramaley (1927) concludes that there is little change of size and habit of growth in alpine plants when they are grown at lower altitudes, and that the altitudinal distribution of species depends largely upon structural differences which adapt the species to the several climatic belts of the mountains. Bonnier (1920) found that lowland species transplanted in the same soil to higher altitudes, after 30 years resemble typical alpine species of the same genera.

Of 170 alpine species identified in the mountains of Colorado by Holm (1927) 63 occur in the arctic and 31 are circumpolar in distribution. He concludes: "The alpine vegetation thus comprises four distinct elements, namely: circumpolar, arctic, alpine, and lowland species."

SELECTION OF STATIONS FOR THE STUDY OF FACTORS OF THE ENVIRONMENT

The climatic factors studied were: evaporation, wind velocity, rainfall, air temperature, and relative humidity. Stations containing standard instruments to determine these factors were maintained at 3 different altitudes. Records were started June 19, 1935, immediately after the opening of the Trail Ridge road above timberline, and continued until August 31. Briefer observations and recordings were made of the mechanical structure of the soil, and of soil moisture and soil temperature.

The lowest recording station was located at Camp Olympus, Estes Park, Colorado, at an altitude of 8,000 feet, near the upper limit of the foothill belt. The instruments were placed in an open and nearly level situation, well beyond the margin of the western yellow pine forest.

The intermediate station was located in the montane belt at an elevation of 10,000 feet near the Trail Ridge road, about 14 miles from Estes Park village. An open, north slope beyond the edge of an Engelmann spruce-alpine fir forest, was selected for installation of the instruments.

The highest station was located at an elevation of 11,500 feet in the alpine belt, near the continental divide just south of Iceberg Lake on the Trail Ridge road. At this station the instruments were placed on an open, dry, gently sloping alpine meadow with a southwestern exposure.

It is well established that even at the same altitude, differences of exposure result in considerable differences in the readings obtained from standard instruments. Every effort was made to select locations which would be as nearly comparable as possible.

ENVIRONMENTAL FACTORS

Evaporation

The rate of evaporation was determined at each station by the use of Livingston white cylindrical porous-cup atmometers, operated in duplicate. Readings were made each week, and the losses reduced to those

of the standard cups. The evaporation data are complete except for three readings lost because of damage to the instruments by rodents.

For the entire 2.5 months period the averages of the weekly readings were: foothills, 192.53 cc.; montane belt, 134.53 cc.; and alpine belt, 90.48 cc. The average daily readings were: foothills, 27.92 cc.; montane belt, 19.22 cc.; and alpine belt, 11.81 cc. The daily average was much greater at the foothill station, being more than 2.5 times as great as at the alpine station, with the evaporation intermediate at the montane station. The greatest variation in readings from week to week occurred in the foothills.

TABLE 1. Average weekly evaporation in cubic centimeters.

Week ending	Foothills	Montane belt	Alpine belt
June 22	119.79	......	147.87
June 29	310.86	242.60	102.30
July 6	335.94	......	......
July 13	114.84	64.02	42.22
July 20	139.76	94.38	55.97
July 27	190.74	125.07	88.07
Aug. 3	175.56	136.29	101.88
Aug. 10	209.88	166.32	55.53
Aug. 17	222.25	166.32	140.06
Aug. 24	184.14	121.11	98.51
Aug. 31	124.08	94.71	72.41
Average	192.53	134.53	90.48

These data are in essential accord with those of Clements and Goldsmith (1924) working in the Pike's Peak region, and with those of Whitfield (1932, 1933) in the same region. However, the data of the latter are partly in accord with those of H. Bath,[1] who, working in 1934, found that the rate of evaporation in the alpine belt was slightly greater than in the foothills, apparently an unusual condition produced by the extreme dryness of the summer of 1934.

Elevation has no direct bearing upon the rate of evaporation (Table 1), but operates through its effects upon other factors, such as temperature, humidity, and precipitation.

Although an increase in evaporation rate may usually be expected to accompany any considerable increase in wind, in Rocky Mountain National Park the effect of wind upon the rate of evaporation is more than balanced by certain other factors. Among these are the increase in precipitation and relative humidity and the decrease in temperature which accompany increases in altitude (see sections on these factors). The net result is that increases in elevation are accompanied by decreases in the evaporation rate. A corresponding decrease in the rate of transpiration of plants from the foothills to the alpine belt has been determined by Whitfield (1932) by the use of phytometers and by Sperry (1936) by the use of potometers.

[1] From unpublished data by Howard Bath.

WIND

Wind velocity was measured by standard anemometers of the Weather Bureau type, with the rotating cups 18 inches above the ground. They were read twice a week at each station.

The average weekly wind movement was greatest at the alpine station, lowest at the montane station, and intermediate at the foothill station. The average hourly wind velocities were: alpine belt, 4.5 miles; foothills, 3.66 miles; and montane belt, 3.16 miles.

The average maximum weekly readings were: alpine belt, 1286.9 miles; foothills, 1050 miles; and montane belt, 948 miles. There was a much greater variation in the average minimum weekly movements: alpine belt, 427.0 miles; montane belt, 103.0 miles; and foothills, 59.2 miles.

Still greater difference in wind velocity between the foothills and the alpine belt were recorded for the summer of 1934;[2] the average wind velocity was 1.27 miles per hour for the upper foothills and 6.55 miles per hour in the alpine belt.

TABLE 2. Weekly wind velocity in miles.

Week ending	Foothills	Montane belt	Alpine belt
June 29	875.2	137.9	565.2
July 6	966.1	361.0	1001.8
July 13	240.7	948.5	480.0
July 20	59.2	180.0	862.6
July 27	695.3	937.5	732.6
Aug. 3	170.0	503.0	871.5
Aug. 10	958.5	103.0	522.0
Aug. 17	235.0	737.0	427.0
Aug. 24	1050.0	875.0	743.0
Aug. 31	912.4	630.7	1286.9
Average	616.24	541.36	749.26

RAINFALL

The amount of precipitation was determined by the use of a standard rain gage at each station. The greatest rainfall was recorded in the alpine belt (Table 3), the least in the montane belt, with the foothills intermediate. Total precipitation for the period June 22 to August 31 was: foothills, 6.66 inches; montane belt, 6.45 inches; and alpine belt, 7.72 inches.

The amount of rainfall usually increased with altitude, although occasionally the foothill precipitation exceeded that of the montane belt. Of the three stations, the montane had the least variable weekly distribution. The heaviest rainfall occurred during the middle part of the growing season.

Whitfield (1933) and Clements and Goldsmith (1924) found that summer rainfall increased directly with altitude. These data are in accord with those of the U. S. Weather Bureau (1934). Weather Bureau estimates likewise show a corresponding increase in winter precipitation from the foothills to the alpine belt. At all altitudes run-off is greatly reduced by the slow melting of snow in spring and

[2] From unpublished data by Howard Bath.

TABLE 3. Amount of weekly rainfall in inches.

Week ending	Foothills	Montane belt	Alpine belt
June 29	0.01	0.03	0.06
July 6	0.52	0.88	0.72
July 13	0.55	1.23	1.12
July 20	2.34	0.92	1.82
July 27	0.12	0.82	1.25
Aug. 3	1.16	0.95	1.20
Aug. 10	0.16	0.27	0.25
Aug. 17	0.50	0.37	0.50
Aug. 24	0.78	0.57	0.26
Aug. 31	0.52	0.41	0.54
Total	6.66	6.45	7.72

early summer, but this effect is, of course, greatest at higher elevations.

AIR TEMPERATURE

A continuous record of temperature in Fahrenheit degrees was obtained at each station by means of a standard hygrothermograph. Average day temperatures were: 66.86° F. for the foothills, 60.08° F. for the montane belt, and 46.21° F. for the alpine belt. Average day temperatures reached a maximum in late July and decreased gradually thereafter, especially in the foothills. The alpine temperatures were consistently lower than those of the montane belt, and the latter usually lower than those of the foothills.

The average night temperatures were lower than the day temperatures at all three stations, although the differences in temperature between day and night decreased with increases in altitude. The average of readings for the night temperatures were: foothills, 49.72° F.; montane belt, 48.47° F.; and alpine belt, 36.22° F. In the alpine belt the air was almost continuously cold, averaging consistently between 40° and 50° F. in the daytime and between 30° and 40° F. at night for each week during the entire summer.

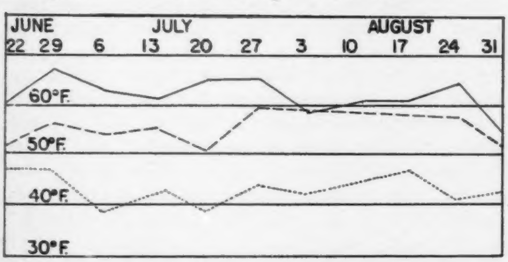

FIG. 1. Average daily temperatures at the three stations: foothill, solid line; montane, broken line; alpine, dotted line.

Average daily temperatures (Fig. 1) for the season at the three stations were: 61.93° F. for the foothills, 55.77° F. for the montane belt, and 42.88° F. for the alpine belt.

The mean weekly temperatures computed upon the daily maxima and minima, reveal the fact that the extremes of temperature were greatest in the foothills, with an average daily variation of 31.25° F., intermediate in the montane belt (variation 22.61° F.), and least in the alpine belt (variation 20.88° F.). However, both day and night temperatures in the alpine belt were constantly low. Here the temperature was near the freezing point nearly every night during the summer. Moreover, the number of days between the latest killing frost in the spring and the earliest killing frost in the autumn is decidedly limited.

These temperature data are in accord with those of Clements and Goldsmith (1924) and Whitfield (1933) working in the Pike's Peak area, with unpublished data of H. Bath (1934) working in Rocky Mountain National Park, and with the records of the U. S. Weather Bureau (1934).

RELATIVE HUMIDITY

Continuous records of humidity were obtained at the three stations from hygrothermographs protected by appropriate shelters. Average day relative humidities for the season at each station were: foothills, 57.16 percent; montane belt, 57.21 percent; and alpine belt, 60.93 percent. Average night humidities for the foothill, montane, and alpine stations for the season were: 83.92 percent, 72.34 percent, and 65.56 percent, respectively.

While the average night humidities at any one station were not consistently above those of any other station, there was a tendency for the alpine station to have a greater number of nights when the relative humidity approached the saturation point. Day humidities increased and night humidities decreased with increases in elevation.

The daily relative humidities (Fig. 2) for the season were: foothills, 66.87 percent; montane belt, 62.76 percent; and alpine belt, 63.33 percent. However, during the first half of the summer the relative humidity of the alpine belt was distinctly lower than that of the foothills, while the humidity of the montane belt was intermediate. During the second half of the summer conditions were reversed; the humidities recorded in the alpine belt were definitely higher

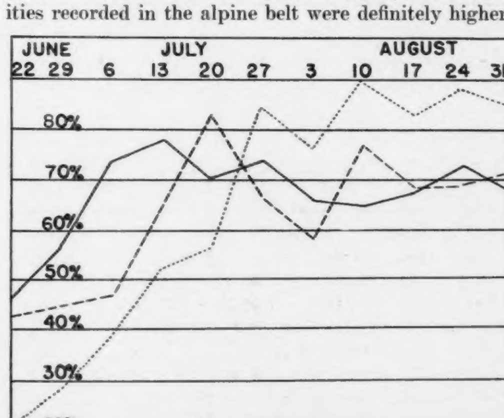

FIG. 2. Average daily relative humidities at the three stations: foothill, solid line; montane, broken line; alpine, dotted line.

than those of the foothill and montane belts, with the graphs for the latter stations showing much intercrossing.

These data on relative humidity are essentially in accord with those of Clements and Goldsmith (1924), and Whitfield (1932, 1933) working in the Pike's Peak area, with unpublished data of H. Bath (1934) working in Rocky Mountain National Park, and with the records of the U. S. Weather Bureau (1934).

Soil Factors in the Foothills

While no mechanical analyses of mountain soils were made, the soil at the foothill and alpine stations (the two stations where root excavations were made) may be described rather accurately from observation.

At the foothill station the soil consisted preponderantly of coarse sand and gravel intermixed with smaller amounts of clay and silt. Chemical analyses made by Hanson, Love, and Moriss (1931) show that such mountain soil contains a high percentage of nitrogen and an extremely high percentage of lime.

Water content of the soil varied at the different locations where roots were excavated. In general the soil in the foothills was very dry, especially on south slopes, with the exception of the few localities where excavations were made along streams or beside lakes.

Soil temperatures at the foothill station were taken on August 6 at intervals of two hours from 8:00 a.m. to 8:00 p.m., at the surface, and at depths of 4, 6, and 12 inches. Figure 3 shows that at a depth of 12 inches the day temperature of the soil ranged between 61° and 68° F., and that a temperature slightly

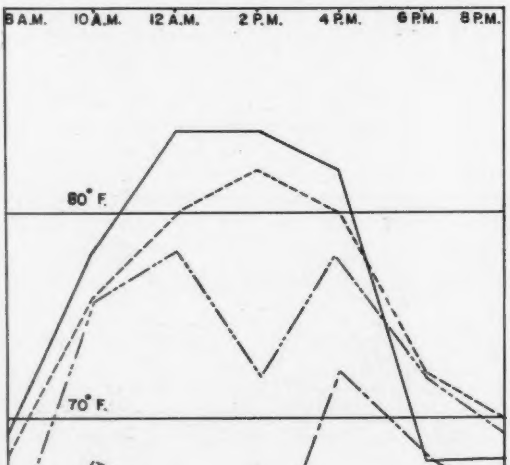

Fig. 3. Soil temperatures at the foothill station. The four graphs starting at the top and proceeding downward represent the surface, and depths of 4, 6, and 12 inches, respectively.

above 70° F. was reached only for a short time in the late afternoon. At a depth of 6 inches soil temperatures ranged from 72° to 80° F. during most of the nine-hour daylight period. At the surface and at a depth of 4 inches, temperatures ranged above 80° F. for four or more hours. Soil temperatures decreased rapidly at all depths with nightfall and remained at 70° F. or lower until the following morning.

Soil Factors in the Alpine Belt

Coarse sand, gravel, and larger rocks, mixed with a peaty mass of undecayed roots characterizes the soil of the alpine belt. The roots of dead plants decay with extreme slowness because soil bacteria are relatively inactive until a temperature of 50° F. is reached. Such a soil temperature is infrequently recorded in the alpine belt except at the soil surface.

The following soil temperatures recorded at Iceberg Lake (altitude about 12,000 feet) on July 26, 1933, are characteristic. At 10:00 a.m. the soil surface registered 65° F.; at a depth of 4 inches the temperature was reduced to 45° F., and at 6 inches to 44° F. At 1:30 p.m. 63° F. were recorded at the soil surface, 47° F. at a depth of 4 inches and 45° F. at a depth of 6 inches. Although the soil usually shows signs of moisture (the recorded annual rainfall is often 30 inches or more at many points between altitudes of 11,500 and 12,000 feet) absorption by plants is at a minimum because of the extreme coldness of the soil.

ROOT HABITS OF FOOTHILL PLANTS

Methods of Investigation

A list of 30 representative herbaceous flowering plants of the foothill and montane belts was compiled. Representative individuals of each species were located in their normal habitats. Measurements were made of the extent of the plants above ground, and the underground systems were carefully excavated, measured, and drawn to scale on coordinate paper. Thus the exact location of the roots in the soil was recorded.

On account of the abundance of rocks and gravel in the soil, excavation proved to be a laborious and time-consuming process. Frequently one or more plants would be excavated hurriedly to find the general type of underground system of the species, thus making less difficult the recovery of complete root systems.

Root Systems, General Considerations

All of the plants studied were perennials. This is accounted for by the shortness of the growing season. Although the period between the last killing frost in the spring and the first in the fall may sometimes be extended to about 115 days in the neighborhood of Estes Park where excavations were made, the effective growing season averages only about 90 days. Nearly all annuals have been eliminated, since the short growing season often prevents the production of viable seed and also interferes with successful germination.

Of the 30 underground systems investigated, 19 were taproots. Fourteen of these were deep enough to reach a permanent water supply and enable the plants to grow in otherwise very deep habitats.

The five species with shallow taproots displayed a lateral spread of roots far greater than the vertical depth; these adaptations take advantage of the frequent light showers typical of the area. Transpiration is probably reduced in many of the mountain plants by the development of a bluish waxy bloom on the leaves or by reduction in the size of the leaf blades. Where vegetation is abundant the landscape often assumes a silvery cast.

Of the 30 plants studied, six were provided with rhizomes. Multiplication by this method is obviously advantageous when seed production and germination are hazardous. Certain native plants, that is various species of Labiatae, may spread so rapidly by means of rhizomes as to be rated weeds in cultivated fields in the mountain parks.

Three bulbous species and one with a corm were encountered. In such species sufficient food is stored to carry the plant through the winter season. Moreover, the storage of food in bulbs and corms permits plants to live in extremely dry habitats. Species having bulbs and corms are relatively numerous in recently burned-over areas.

Few fibrous-rooted herbs are found among mountain plants. Grasses with fibrous roots are confined to bottom lands and other moist places. The only fibrous-rooted plant included in this study was *Sedum stenopetalum* Pursh, a succulent species so small that its shallow fibrous system of roots is sufficient to enable it to exist even under very dry conditions.

ROOT SYSTEMS; TAPROOTS

Arenaria fendleri Gray occupies dry, rocky and sandy areas in the open, but is also frequently abundant under *Pinus scopulorum* (Engelm.) Lemmon. The elaborate underground system (Fig. 4A), excavated on a dry western slope, reaches a depth of 46 inches with a spread of 2 feet. Each small secondary root ended in a mass of fine branches which penetrated the smallest crevices in the rocks. The tough and rope-like root seemed well adapted to the excessively dry habitat. Near the soil surface the main root divided into 4 broad sections, each bearing a tuft of several leaves together with a flowering stalk 5 inches high. This species is one of a few foothill plants which ascend above timberline, in which habitat both the root system (Fig. 4B) and the stems are of the same general type as in the foothills but greatly reduced in extent; in the alpine belt the multicipital taproot extended into the dry, rocky soil to a depth of 15 inches and gave rise to several leafy tufts so closely placed as to give the effect of a cushion. The plant shown in Fig. 4B had 9 stalks from 2 to 3 inches high. Where moisture is more abundant *Arenaria fendleri* is crowded out by other species.

The plant of *Arnica pumila* Rydb., whose root system is pictured in Fig. 5A, had two stalks, 24 and 26 inches in length, respectively, each with a large flowering head. Coarse sand and small rocks prevailed in the soil. The primary taproot measured

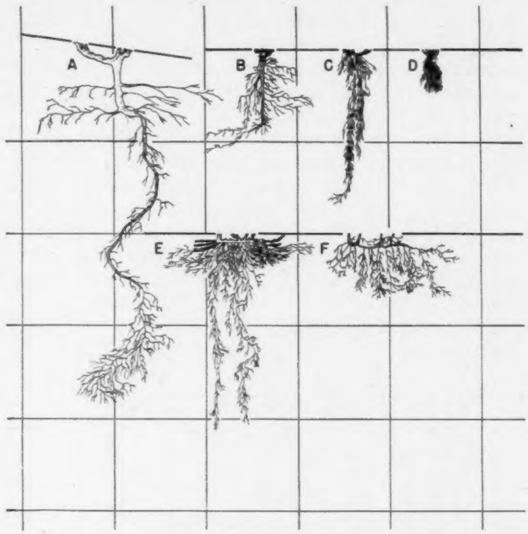

FIG. 4. Underground systems of plants of the foothill and alpine belt: A. *Arenaria fendleri* (foothills), B (alpine belt); C. *Sedum stenopetalum* (foothills), D. (alpine belt); E. *Achillea millefolium* (foothills), F. (alpine belt).

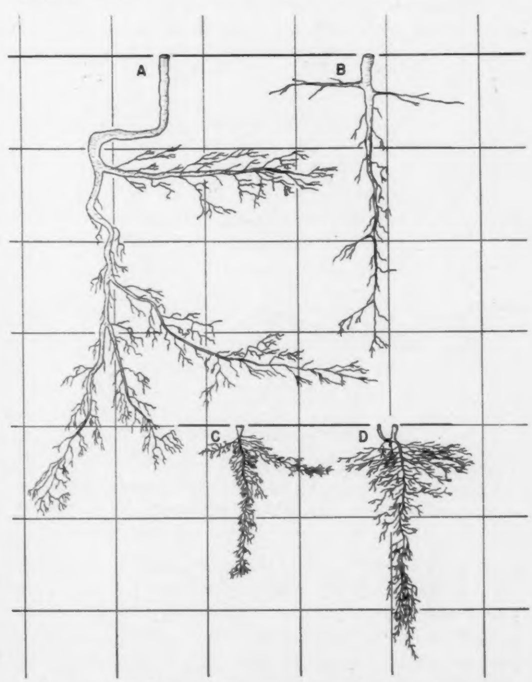

FIG. 5. Underground systems of foothill plants: A. *Arnica pumila*, B. *Oreocarya glomerata*, C. *Grindelia squarrosa*, D. *Gaillardia aristata*.

half an inch in diameter at the soil surface and tapered gradually as it reached lower depths. Although its total depth was 56 inches, there were few but large secondary roots. A loose covering, resembling deteriorated bark, masked the pure white color of the brittle living portion of the root. The large size of the underground system permits storage of quantities of food and assists the species to withstand the relatively severe environment.

Chamaenerion angustifolium (L.) Scop., one of the pioneers to invade burned-over forest areas in the Rocky Mountain, is adapted to dry surface habitats through its development of a root system deep enough to reach a permanent water supply. Under especially favorable conditions, the flower stalk may reach a height of 3 feet. A small group of plants, whose four flower stalks measured 15 inches in height, was selected for investigation. All were connected underground with a single taproot (Fig. 6C), which

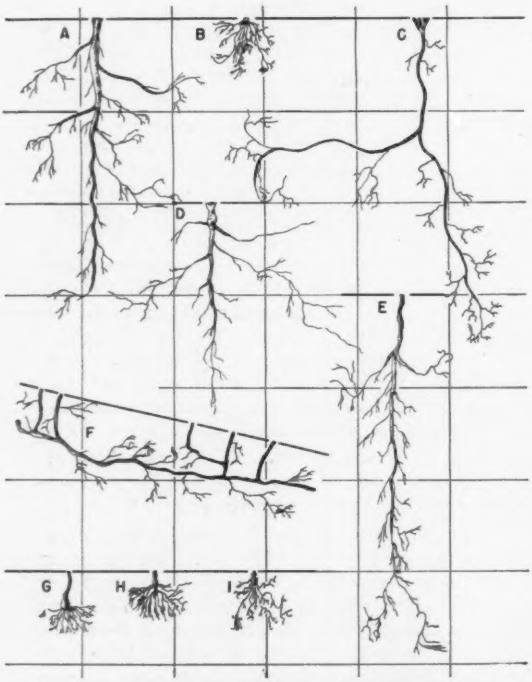

Fig. 6. Underground systems of foothill plants: A. *Geranium fremontii*, B. *Dodecatheon pauciflorum*, C. *Chamaenerion angustifolium*, D. *Erigeron alatum*, E. *Lychnis drummondii*, F. *Anogra coronopifolia*, G. *Calochortus gunnisonii*, H. *Allium cernuum*, I. *Zygadenus elegans*.

extended to a depth of 42 inches. With the exception of the one main secondary root, the laterals were small and few in number. Like many of the larger rooted plants of the foothills, the root was tough in texture and the color a light tan. Examination of numerous other clumps of fireweed disclosed that in every case the entire clump was connected in the upper soil levels by branching rhizomes. Weaver (1919) found that this species reaches a depth of 35 to 48 inches on moist slopes in the half shade of Douglas fir and mountain maple.

Erysimum asperum DC. was studied in a typical gravelly clay loam sod surrounded by grasses and other herbaceous vegetation. Plants investigated were about 2.5 feet in hight, freely branched, and in full bloom. The taproot (Fig. 7G) extended vertically

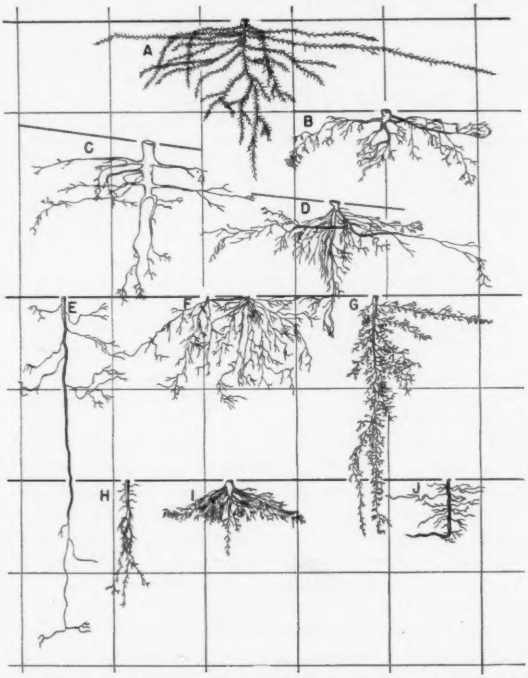

Fig. 7. Underground systems of foothill plants: A. *Pentstemon unilateralis*, B. *Castilleja linariaefolia*, C. *Onagra strigosa*, D. *Artemisia frigida*, E. *Potentilla gracilis*, F. *Aster commutatus*, G. *Erysimum asperum*, H. *Mertensia ciliata*, I. *Rudbeckia hirta*, J. *Stachys palustris*.

29 inches, with a lateral spread of 12 inches. Secondary roots were plentiful but short. The entire underground system was rather tough, flexible, and tan in color. The root is well adapted in form to secure firm anchorage, successful competition for nutrients and water in a sod, and for food storage.

Eriogonum alatum Torr. is typical of sandy meadows, dry at the surface but with abundant moisture at lower soil levels. A typical plant had a single branched flowering stalk 3 feet high. The taproot (Fig. 6D) reached a depth of 25 inches with a total horizontal spread of 32 inches. The root was devoid of fine branches and was tough and rope-like in structure.

Eriogonum umbellatum Torr., one of the commonest of the sulphur flowers of the Rocky Mountains, grows in dry, sandy or rocky areas on south slopes in the foothill and montane belts. The 71 flower stalks of a plant excavated, averaging 13 inches in

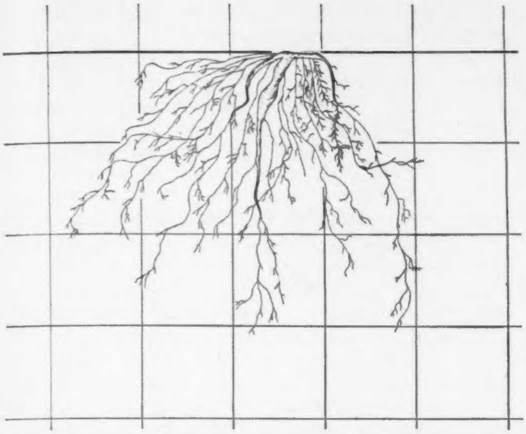

FIG. 8. Underground systems of foothill plants: *Eriogonum umbellatum.*

height, caused a widening of the root (Fig. 8) at the surface of the ground. Below a depth of 8 inches, the root tapered gradually to a minimum diameter which characterized it to its termination at a depth of 41 inches. The numerous laterals had a total spread of 48 inches. The root system was tough, dark brown in color, and with a heavy bark; it is so constructed that it may penetrate the hard and rocky ground and endure severe and varied environmental conditions.

Gaillardia aristata Pursh prefers a rich, black loam, although it frequently becomes established in loose sand above rich soil. The plant pictured in Fig. 5D extended its brittle root downward 30 inches. Its numerous, well-branched laterals spread 17 inches in the surface foot of soil but were not extensive at lower levels. Above ground the plant displayed two flower stalks 20 inches high, each attached to its own division of the root. Although the underground parts are neither deep enough nor of sufficient extent to support a large plant or to store food for it, they are adequate for a perennial which is limited in the number and size of its flower stalks.

Geranium fremontii Torr. is sometimes found in open pine forests or among aspens, although it is most successful in its retreats on dry slopes where competition is greatly reduced. A typical plant had 3 flower stalks only 7 inches high, supported by a long, rope-like taproot (Fig. 6A) which reached a depth of 34 inches. The roots were twisted and dry, and protected by a dry, partly decayed cover. Each flowering stalk had a partially separate root, but several of these were twined around each other and protected by the common cover. The root system was extremely brittle and therefore difficult to excavate under the unusually dry and rocky conditions. The numerous secondary roots terminated in many fine branches when they reached areas which were somewhat less dry.

Grindelia squarrosa (Pursh) Dunal, a perennial herb of the Great Plains, whose seeds have been carried by various agents throughout the foothills, may be found at altitudes up to at least 10,000 feet. The taproots of typical plants (Fig. 5C) reached a depth of 20 inches with a lateral spread of 17 inches. The only secondary roots of importance were close to the soil surface. The root was heavy, light yellowish brown in color, with no protective covering, although it seemed to have no difficulty in penetrating through a soil consisting of dry sand and gravel. Above ground the freely branched stem reached a height of 13 inches. The plasticity of the gumweed is suggested by the description of its roots as found by Weaver (1919) in true prairie, in which habitat the underground parts not only reached depths of 50 to 73 inches, but also developed numerous laterals with abundant rootlets.

Lychnis drummondii Wats. was excavated in its typical habitat, the moist, sandy bank of a stream. A vertical root (Fig. 6E), extending to a depth of 47 inches, anchored the plant. The few secondary roots were heavy in structure and not much branched. The entire underground system was brown in color, tough enough to permit penetration into hard soil and extensive enough to store adequate food for a perennial. Three leafy stalks 9 inches long and a single flowering stalk 12 inches high completed the plant above ground. Other individuals studied in a much drier habitat displayed the same type of root system but reached a depth of only 2.5 feet.

Mertensia ciliata (Torr.) Don. occupies moist roadsides and stream banks. In such habitats adequate moisture may be secured without an extensive root system. The average taproot (Fig. 7H) reached a total length of 16 inches and had few secondary roots. Plants excavated in somewhat drier areas had more laterals. In all habitats the roots were tough; they varied from light tan to dark brown in color. Other species of Mertensia in dry habitats had somewhat more extensive roots, although the general form was the same in all that were investigated.

Oreocarya glomerata (Nutt.) Greene usually occupies sunny, sandy slopes. The large taproot of an average plant grew to a depth of 3 feet, with few secondary roots except in the upper 6 inches of dry soil. A scaly, protective sheath, brown in color, covered the entire root. Excavation was made easy by the tough texture of the root under the covering. The flower stalk, although characteristically coarse, averaged but 22 inches high; the plant was considerably more extensive underground than above.

Phacelia glandulosa Nutt. was excavated from its typical dry roadside habitat where it grew in rich, sandy loam. The extensive underground system (Fig. 9) consisted of a short taproot which divided at a depth of about 6 inches into several much branched extensions, some of which permeated downward through 4 feet of soil. The horizontal spread was 40 inches in its widest section in the upper foot of soil. Above ground the plant reached a height of but 22 inches, although it was coarse and much branched. In such a dry soil and severe habitat an

extensive absorbing surface and storage roots are of distinct advantage.

Potentilla gracilis Dougl. extended its long taproot (Fig. 7E) to a depth of 42 inches in moist, heavy, black loam, on a dry creek bank. The root was tough, flexible, light tan in color, and with few well-developed secondary branches. Average plants had two flower stalks, 12 and 15 inches high, respectively. This was the only species of Potentilla included in the study, although incomplete excavations of several other species indicate that many members of the genus have deep storage roots and also that they prefer a moist, rich soil.

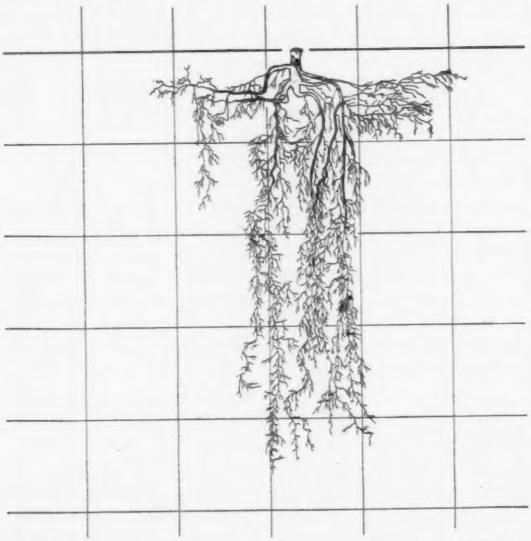

FIG. 9. Underground systems of foothill plants: *Phacelia glandulosa.*

ROOT SYSTEMS; SHALLOW TAPROOTS

Artemisia frigida Willd. is one of the few plants of the Great Plains which is distributed abundantly in the mountains, where it is common in rocky soil in the foothill and montane belts and is frequently found at even higher altitudes. The plant whose root system is shown in Fig. 7D had 9 leafy stalks averaging 15 inches in height. The horizontal spread of the roots was 36 inches, nearly double the depth. Such an underground system is well constructed to take advantage of frequent light showers. At the same time the toughness and stockiness of the roots enable them to endure the severe conditions of the winter months in the mountains. The wide distribution of the species under both plains and mountain climates testifies to its ability to maintain itself under varied and severe conditions. Weaver (1919, 1920) found that at Colorado Springs at an elevation of about one mile, the root of the Arctic sage reached an average depth of 4 to 6 feet. However, the same profuse branching of the roots which characterizes the species at higher altitudes occurred also at Colorado Springs and in the mixed prairie at Limon, Colorado.

Castilleja linariaefolia Benth., the common red paint brush of the upper foothill and lower montane belts, was excavated from among the sagebrush on a dry, sandy roadside. The soil was exceedingly dry to a depth of more than two feet. Average plants had 4 flowering stalks with a mean height of 19 inches. The tough, rope-like roots (Fig. 7B) extended downward but 10 inches; their lateral spread was 2 feet. Numerous branches arose from the several secondary roots which in turn grew from the short, thick primary root. The closeness of the roots to the soil surface makes it possible for them to take advantage of the light rains. In addition they are tough and elastic enough to withstand the severe winter climate.

The biennial *Onagra strigosa* Rydb. was studied in its typical dry, sandy and rocky habitat on a sunny, south slope, at an altitude of 7,500 feet. The typical plant was freely branched at the base, with 6 main stems averaging 15 inches in length, the longest extending 2 feet above the ground.

The coarse taproot (Fig. 7C) reached a depth of 21 inches. The numerous, branched laterals were coarse and rope-like; their total spread was 30 inches. The root system resembles to a considerable extent that of some of the large composites such as the arnicas and rudbeckias. It is admirably adapted to the storage of food, enabling the plant to send up a large flowering stalk in the second season.

Pentstemon unilateralis Rydb. is abundant in fields and on hillsides at elevations of 7,000 to 8,000 feet, where it occupies fairly moist slopes on which black loam has accumulated. The roots (Fig. 7A) were fine but tough, the taproot reaching a depth of 21 inches, and the numerous laterals spreading to a total breadth of 54 inches. Nearly the entire root system occupied the upper foot of soil; the numerous, short, tertiary roots were well placed for absorbing moisture from light rains. Typically there are 5 stalks above ground, with an average height of 25 inches.

Rudbeckia hirta L. frequents moist and fertile mountain meadows. A representative plant was excavated from the bank of a small stream where it was growing in soil that was moist except for the upper 3 inches. Above ground there was a single flowering stalk extending to a height of 20 inches. The sturdy but short taproot (Fig. 7I) permeated the soil to a depth of only 8 inches, but the numerous and much branched secondary roots spread laterally more than twice that distance. The upper 6 inches of soil was well occupied by roots, as would be expected of a species which lives in moist areas. Although the underground system was not heavy in structure, it was sturdy and extensive enough to supply the plant with moisture and nutrients and to give it adequate anchorage.

ROOT SYSTEMS; RHIZOMES

Achillea millefolium L. is one of the few species of the Great Plains which has made its way up the canyons to altitudes above timberline. In the mountain area it is typically found along roadsides, indi-

cating the probability that its seeds have been carried upward through the canyons by passing automobiles. Specimens were excavated along the roadside at an altitude of 8,000 feet. Here the plant was growing abundantly in dry, rocky, and sandy soil. An elaborate root system (Fig. 4E) extended from an equally intricate branching rhizome which grew in the upper two inches of soil, forming the underground connection for large clumps of stems. The fine but tough roots penetrated the dry soil to a depth of 25 inches; the upper 6 inches of soil was well occupied by them. Numerous flowering stalks extended from 11 to 18 inches above the ground line. Plants of this species, studied on an exposed slope in moist, rocky soil in the alpine meadows above timberline (Fig. 4F), had the same elaborate rhizome system with numerous stalks in the clumps, but were considerably reduced in extent both above and below ground. Typical alpine plants had only 4 flowering stalks ranging from 2.5 to 4 inches high; the much branched rhizomes gave rise to numerous much branched roots extending to a depth of 8 to 9 inches from the surface of the soil. In all mountain climates, but especially in the alpine belt, perennials with the rhizome habit have an obvious advantage over species which depend upon reproduction by seed.

The rhizomes (Fig. 7F) of *Aster commutatus* Gray occur at the soil surface and give rise to stems at frequent intervals. Sometimes the distance between stalks is so much reduced as to give the effect of a broad tuft of stems, however, the entire tuft is connected underground. Branched secondary roots extend in every direction from the main roots, completely occupying the surface foot of soil. The greatest depth measured in the plants excavated was about 14 inches, with a horizontal spread which varied with the number of stems growing from the rhizome system. The finer roots were easily broken but the larger ones were tough and pliable. Since the species is late in blooming, the production of viable seed is hazardous and migration must usually depend upon extension of the rhizome system. The flowering stems averaged 7 inches in height. *Aster commutatus* usually is found in moist soil and the underground system pictured was obtained from soil which was moist below the 6 inches level.

Monarda menthaefolia Graham grows in large colonies in moist habitats, often in or near aspen groves. Colonies were studied on the roadside in the partial shade of aspens, in moist soil which was dry only at the surface. The elaborate root system (Fig. 10B) was connected by coarse rootstalks which extended parallel with the soil surface in the upper 3 inches of soil. A network of fine roots extended downward 3 to 6 inches from the lower side of the much branched rhizome. At intervals tough, heavy roots grew from the rhizome to depths of 4 feet or more. Frequent branched laterals turned from the taproots nearly at right angles. New lateral and terminal buds are formed on the rhizomes from year to year and thus each new generation of stems is carried farther from the parent, with which it maintains continuity in-

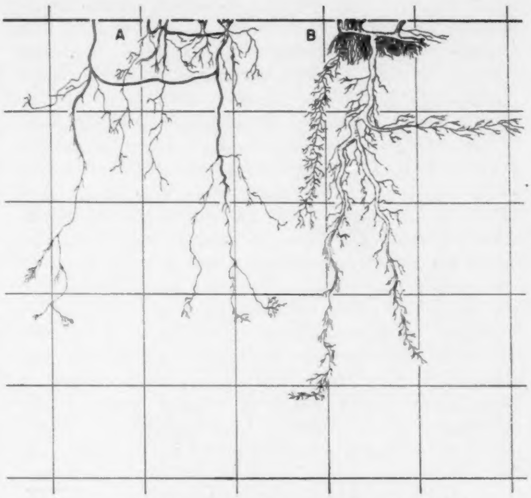

FIG. 10. Underground systems of foothill plants: A. *Solidago decumbens*, B. *Monarda menthaefolia.*

definitely. The taproots are large enough to store considerable food. The perennial habit, the toughness and extensiveness of the root system, and the elaborate branching of the rhizomes, make it possible for Monarda to persist under the relatively severe conditions of the Rocky Mountain climate. Above ground the flowering stalks measured approximately 15 inches each.

Anogra coronopifolia (T. and G.) Brit. occupies roadsides and near-by disturbed areas, where it blooms in the foothills in late June and early July. On the plains at Denver it is in full bloom during the last week in May. This is evidently a plains species which has been carried up the canyon into the foothills by way of the roadsides. The plant is usually found in great clumps which are connected underground by an elaborate system of branching rhizomes (Fig. 6F). Several groups were studied on the banks of a creek bed not far from the main road, where they grew in moist sandy soil almost devoid of rocks. The rhizome system was well developed at a distance of 6 to 8 inches below the ground level. Much branched rootstalks reaching a length of 4 to 5 feet were not uncommon; they were tough, flexible, tan in color, with a light protective covering. Delicate, branched roots extended downward from the rhizomes. Upright stem bases grew upward from the rhizomes and branched into numerous flowering stems near the soil surface. Two to 6 flowering stems grew from each stem base and the individual flower stalks ranged from 6 to 12 inches in length. *Anogra coronopifolia* exhibits identical underground habits on the plains at Denver, with practically no difference in size or extension of parts either below or above ground. The species is admirably adapted for slow invasion of new areas without depending upon the production of seed.

Solidago decumbens Greene was excavated from a dense group of plants occupying moist soil on the

south slope of the bed of a mountain stream at an altitude of 7,500 feet. Long, tough, flexible, dark brown, rope-like rhizomes (Fig. 10A) branched through the soil at depths varying from 2 to 8 inches. Tough, rope-like roots extended downward from the rhizomes at intervals of several inches; the greatest depth measured was 42 inches. Flowering stems grew upward from the root bases. From the first base there were 4 flowering stalks with an average height of 11 inches; from the second there was one stalk 5 inches high; from the third 2 stalks 10 and 11 inches in height respectively; and from the fourth one stalk 7 inches high. The elaborate rhizome and root system, together with the perennial habit, insure the success of this species at all altitudes and in practically all environments, especially in meadows and along roadsides where competition with grasses is keen. Lateness of blooming usually prevents the production of viable seed at higher altitudes.

Stachys palustris L. prefers very moist, sandy soil, free from rocks. Studies of its underground habits were conducted along an old stream bed which afforded considerable protection from wind and excessive light and temperature, but where there was considerable competition with grasses and sedges. The taproot (Fig. 7J) permeated the wet soil to a depth of barely 8 inches. Rhizomes extended laterally from the taproot at several levels in a node-like fashion; their development is no doubt correlated with changes in the water level from time to time during the growing season. A single flowering stalk grows from the top of each taproot.

Root Systems; Shallow Fibrous Roots

Sedum stenopetalum Pursh is common on dry, sandy and stony slopes at all altitudes in the mountains, including the alpine belt. It often frequents rock crevices where it thrives on a minimum of water. The root system (Fig. 4C) was extremely fibrous, extending into the dry soil to a depth of 20 inches with little horizontal spread. Typically, 3 or 4 flowering stalks less than 2 inches in height were connected with each other and with the broadened top of the root. Similar growing habits were exhibited by the species excavated on dry, rocky slopes above timberline (Fig. 4D) except that the plants were less extensive both above and below ground. The success of the species in excessively dry habitats is accounted for by the perennial habit, the relatively great extent of the roots as compared with the tops, and the succulent structure of the stem and leaves.

Root Systems; Corms and Bulbs

Dodecatheon pauciflorum (Durand) Greene is abundant in wet meadows of the montane belt and upper foothills. Studies of its underground habits were made from plants growing on a stream bank among tall grasses and other herbaceous plants which afforded some protection from the sun and wind. In a typical plant a single flowering stem extended to a height of one foot above the corm, which measured nearly 1.5 inches in length. At the base of the stalk above the corm were 6 basal leaves averaging 4 inches in length. Branching roots (Fig. 6B) extended into the wet soil to a depth of 8 inches; the horizontal spread was practically as great as the vertical depth. All of the roots were white and somewhat brittle. The possession of a corm makes it possible to store food which may be used during unfavorable periods or for the production of an extensive early growth in the spring. Since the species is confined to wet habitats, development of a large root system is unnecessary.

Allium cernuum Roth. was excavated from a small elevation in dry, sandy soil, the typical habitat of the species. Many delicate branching roots (Fig. 6H) extended from the bulb but the total depth did not exceed 6 inches, of which the bulb occupied two. The horizontal spread of the roots was as great as the vertical depth. Each bulb produced a single stalk above ground, averaging 6 inches in height. Obviously the storage of food reserves in the bulbs compensates in part for the lack of a better-developed root system.

Calochortus gunnisonii Wats. grows best in rich, sandy soil at the edge of aspen thickets or in sagebrush meadows; in either habitat there is adequate moisture. The bulb and roots are similar to those of *Allium cernuum* except that the bulbs are usually found at depths of 4 to 5 inches below the soil surface. The total depth of the underground system (Fig. 6G) was 9 inches, and the horizontal spread was as great as the depth. The roots were white and brittle. Characteristically, there was above ground a single flowering stalk about 12 inches high.

Zygadenus elegans Pursh occupies rich, sandy soil in sunny exposures at all altitudes. The ovate shaped, tunicated bulbs (Fig. 6I) were located at the soil surface. Brittle, white, branched roots extended downward 5 inches from the bulb and laterally the same distance. Above ground there was a flowering stalk 19 inches high growing from a rosette of 6 long, linear leaves. Bulbous species are not common in the Rocky Mountains, but the wand lily shares with other bulbous plants the ability to store abundant food reserves.

ROOT HABITS OF ALPINE PLANTS

Methods of Investigation

Studies were made of the growth habits of 34 species of alpine plants in the vicinity of Iceberg Lake in Rocky Mountain National Park, at altitudes of 11,000 to 12,000 feet. The study included typical species both in protected and exposed sites as well as in wet and dry habitats.

Measurements were made of the above ground parts of the plants, and the underground systems were excavated through the use of trenches dug far enough from the plants to insure securing a complete root system in each case. The roots and other underground parts were drawn to scale in the exact position in which they grew in the soil. Several plants of each species were excavated and the drawing of the most typical was selected.

The soil from which the plants were excavated was decidedly rocky and the presence of dead but undecayed roots added to the difficulty of making studies of the underground systems.

In the following sections the distributions of alpine plants are taken in most cases from the studies of Theodore Holm.

ROOT SYSTEMS; GENERAL CONSIDERATIONS

The conspicuous vegetation of the alpine belt consists largely of herbaceous flowering plants, most of them less than a foot high. Nearly all are perennials, since the extremely short growing season results either in the production of no seed or of small amounts of seed of low vitality.

Rhizomes constitute the commonest type of underground system, and provide the best means of propagation as well as the best method of food storage in the severe alpine environment. Moreover, the soil temperatures are so low that growth is extremely slow and it is doubtful if annuals have time, in the short growing season, to make sufficient growth to complete their life cycles. The low temperature of the soil seriously interferes with the intake of water by the roots. In exposed situations mat plants are common, since low growth close to the soil surface greatly lessens the deadly desiccating effects of the wind; the entire, much branched mat grows from a single root. Frequently plants with tufts of stems above ground grow from short taproots. Fibrous root systems are infrequent.

ROOT SYSTEMS; RHIZOMES

Rhizomes constitute the most frequent type of underground system in the alpine belt. In some cases these are short, but often they are long and branched, connecting a considerable number of separate above ground stems.

Saxifraga chrysantha Gray is a low, somewhat woody plant, with fleshy leaves arranged in a rosette, terminated by a single yellow flower. The species is confined to the Rocky Mountains and is rarely encountered outside of Colorado and New Mexico. Several plants were excavated from moist, rocky soil, on a north slope. A rhizome 5 inches long (Fig. 11J) gave rise to numerous branched roots which occupied the third and fourth inches of soil. The greatest depth reached was less than 7 inches. Such a root system, although not extensive, is able to make use of the frequent light rains. A new plant originates when the rhizome between it and the original root decays.

Arenaria sajanensis Willd., a low mat plant of circumpolar distribution, is common at altitudes of 11,000 to 13,000 feet in the Rocky Mountains of Colorado. It prefers dry, peaty, and rocky soil, on south slopes. A main taproot (Fig. 11K) grows 2.5 feet downward from a much branched rhizome, which in turn supports the low, leafy mat. The mat of the plant drawn was nearly circular and approximately 8 inches in diameter. Roots subtended by the rhizome make possible the production of new mats after decay of portions of the older parts of the rhizome.

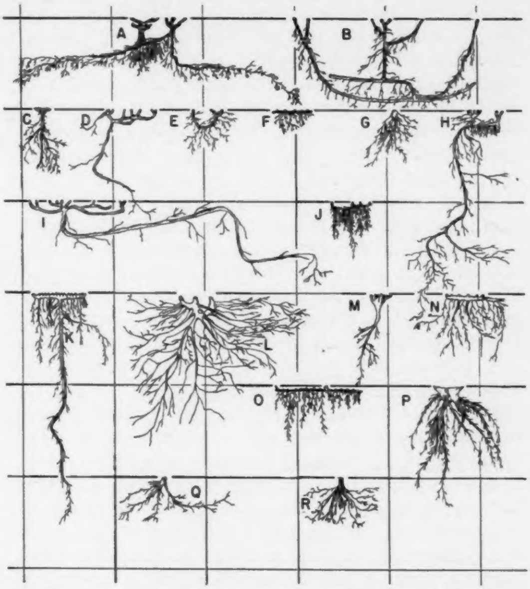

FIG. 11. Underground systems of alpine plants: A. *Dryas octapetala*, B. *Vaccinium scoparium*, C. *Phacelia sericea*, D. *Campanula uniflora*, E. *Veronica alpina*, F. *Polemonium pulcherrimum parvifolium*, G. *Erigeron uniflorus*, H. *Potentilla glaucophylla*, I. *Salix saximontana*, J. *Saxifraga chrysantha*, K. *Arenaria sajanensis*, L. *Sieversia turbinata*, M. *Trifolium dasyphyllum*, N. *Antennaria umbrinella*, O. *Stellaria crassifolia*, P. *Castilleja brachyantha*, Q. *Anemone zephyra*, R. *Primula angustifolia*.

Sieversia turbinata (Rydb.) Greene, known as the North American alpine rose, is among the commonest and most conspicuous of the Rocky Mountain plants of high altitudes. Like *Arenaria sajanensis*, it is circumpolar in distribution, although its abundance in North America indicates its probable origin here. Like many other alpine plants, it was probably stranded at higher elevations in the Rocky Mountains when the glaciers retreated northward. Excavations made in its typical habitat in fairly moist but unprotected rocky and sandy soil, revealed an underground system (Fig. 11L) consisting of a substantial, branched rhizome in the upper 3 inches of soil, with well-developed roots growing from many places on the rhizome to a depth of 18 inches, and with a total root spread of 18 inches. Many excavations of this species were undertaken, since our data on the underground parts do not agree entirely with Holm, who describes the plant as having a deep primary root, with some secondary roots from the rhizome. Again, contrary to his findings, the species was frequently found as single plants or in small clumps rather than in dense mats, and at altitudes as low as 10,500 feet in the Colorado Rockies.

Polemonium pulcherrimum var. *parvifolium* (Nutt.) A. Nels., one of the most delicate of alpine species, was excavated from an exposed east slope, where it grew in moist, rocky soil, partly protected by large

rocks. Individual plants averaged 4 leaves, each less than 3 inches long, and the flowering stalks ranged from 4 to 6 inches in length. The underground parts of the plant were correspondingly poorly developed. A feeble development of branched roots (Fig. 11F) extended to a depth of 2 to 3 inches from a well-developed rhizome placed horizontally practically at the ground line.

Potentilla glaucophylla Lehm. was studied on a north slope in rocky soil, at an altitude of 11,500 feet, where it thrived in competition with grasses. A coarse rhizome (Fig. 11H) in the second inch of soil gave rise to a relatively coarse and well-branched taproot which extended to a depth of more than 2 feet. Numerous plants grew at intervals from a common rhizome, each plant consisting of several leafy flowering stalks from 6 to 9 inches high.

Veronica alpina L. is circumpolar in distribution in addition to its frequent occurrence at high altitudes in the Rocky Mountains. Excavations of the species were made from its typical habitat in very wet, rocky soil, among grasses, at an altitude of 11,000 feet. A woody rhizome reaching to a depth of more than 2 inches subtended a few branched roots (Fig. 11E) which permeated only through the fifth inch of soil. Above ground the flower stalk reached a total height of 5 inches.

Salix saximontana Rydb., a creeping shrub 2 to 3 inches in height, covers large areas above timberline in Rocky Mountain National Park. It is also reported to be common in northern Canada. Excavations were made in both moist and dry rocky soil, at an altitude of 11,500 feet. Areas of the plant many feet in extent were found to have a common connection underground. One portion of such an underground system (Fig. 11I) consisted of a sparsely branched, woody root, growing in the upper 8 inches of soil and roughly parallel with the surface. At intervals of 5 to 15 inches the root gave rise to profusely branched woody stems, the branches growing 1 to 2 inches through the soil before reaching the surface. The absence of roots from the stems in the soil indicated that they are subterranean stems rather than rhizomes, a conclusion concurred in by Warming (1909).

Campanula uniflora L., although circumpolar in distribution, is rarely found in abundance either in the Rocky Mountains or in the Arctic. It usually occurs in small groups of individual stalks from 1 to 3 inches apart, among an abundance of low grasses. Excavations of the species from dry, rocky soil on a north slope at an altitude of 11,000 feet showed that the several stalks in the group are connected underground with a branched rhizome (Fig. 11D). A single taproot served for one or several rhizome groups; the entire underground system rarely reached a total depth of more than 15 inches.

Vaccinium scoparium Leiberg frequently is encountered in such profusion that its stalks are matted together. The stems average about 3 inches high in the alpine belt of the Rocky Mountains and are described by Holm as having the same habit in the Arctic of Greenland and Canada (1922). Excavations from rocky soil on an exposed east slope at timberline revealed a deep and extensive, branched rhizome system (Fig. 11B) in the upper 10 inches of soil, with relatively few short roots growing from all parts of the rhizome.

Dryas octapetala L., the eight-petalled avens, occurs over an enormous geographical range; it is not only circumpolar in distribution, but is also abundant in the alpine belt of the Rocky Mountains and in most of the mountain ranges of central Europe and Asia. Its twisted, woody stems trail along the surface of the ground forming a thick assemblage of shoots scarcely close enough to each other to deserve the name of cushion plant. No doubt the persistence of the elongated plumose styles in the fruits assist greatly in wind dispersal, but probably the plant depends for its local distribution mainly upon the development of an intricate rhizome system. Tough, brownish, multicipital taproots (Fig. 11A) extended downward a short distance, where they gave rise to smaller roots which permeated the upper 6 to 10 inches of soil laterally to a distance of 15 to 18 inches from the taproot. Plants extending over many square feet of surface have a common underground system. The statement of Salisbury (1936) that: "An old mat of Dryas, for instance, which does not rise more than 3 inches above the soil, may have a root that permeates to over 5 feet below the surface," apparently describes the development of the species in a rock garden at low altitude; numerous excavations above timberline in Rocky Mountain National Park disclosed an underground system confined almost entirely to the upper foot of soil.

Achillea millefolium L. (Fig. 4F) is discussed in the section dealing with foothill plants, where its development in the foothills is compared with the species as it occurs in the alpine belt.

Stellaria crassifolia Ehrh., a species of wide distribution through the mountains of western North America, is also found in the Appalachians and in Arctic North America. Excavations were made in a typical habitat on a south slope in damp, rocky soil. The rhizomes (Fig. 11O), which lie just below the surface of the ground, tie together many plants extending over an area several feet in diameter. Many small roots extend from the rhizomes, rarely reaching depths of more than 4 to 6 inches. A prominent feature of the underground system is the abundance of reduced leaves placed with considerable regularity on the rhizome. Leafy stalks 2.5 to 3 inches high grow from the rhizome at intervals of 6 inches or more.

Antennaria umbrinella Rydb. occurs on the higher mountains of western United States at altitudes up to 13,000 feet. Excavations made on an east slope in moist, rocky soil revealed a rhizome just beneath the soil surface (Fig. 11N), with 3-inch stems ascending at intervals of about 1 inch, and with small, branched roots growing at frequent intervals from the rhizome to a depth of 5 to 8 inches. Like *Stellaria crassifolia,*

the rhizomes are characterized by the frequent occurrence of reduced leaves.

Caltha rotundifolia (Ruth.) Greene has its center of distribution in the Rocky Mountains, where it occurs at altitudes of 10,000 feet and above, in cold, wet soils. Frequently the species sends its flowers up through the snow. The very short, vertical rhizome (Fig. 12E) gives rise to numerous tender, white

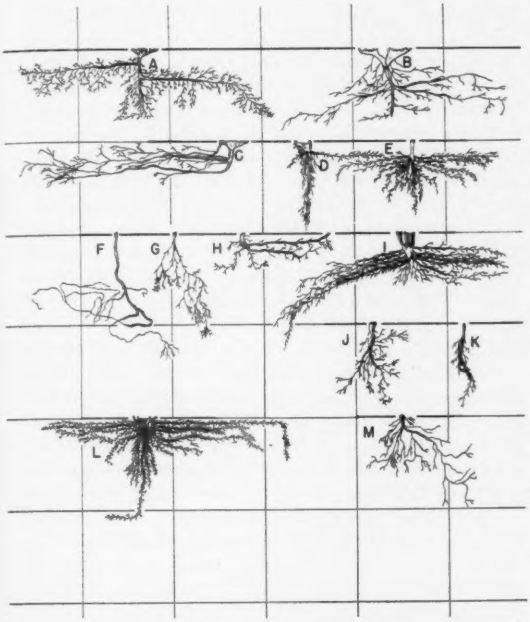

FIG. 12. Underground systems of alpine plants: A. *Phlox caespitosa*, B. *Eriogonum flavum*, C. *Silene acaulis*, D. *Polygonum bistortoides*, E. *Caltha rotundifolia*, F. *Heuchera bracteata*, G. *Rydbergia grandiflora*, H. *Sedum rhodanthum*, I. *Pulsatilla hirsutissima*, J. *Erysimum nivale*, K. *Mertensia alpina*, L. *Pentstemon glaucus*, M. *Senecio taraxacoides*.

roots, which are well provided with short laterals in spite of the cold and excessively wet habitat. The underground system averaged 20 inches in diameter and 10 inches in depth.

Polygonum bistortoides Pursh, one of the most conspicuous flowering plants of Arctic America and Eurasia, is common on moist, sandy, east slopes of the Rocky Mountains. Its blooming season is unusually long for the high altitudes, and its relatively tall flower stalks may be seen from the middle of June until early September. Usually the plant has only one or two flower stalks from 12 to 15 inches high, ascending from a thick, chaffy rootstock (Fig. 12D) from which fine and much branched roots are developed to a depth of 12 inches. Frequently one or more roots in the second or third inch of soil may extend the underground system laterally about one foot in the moist sand.

ROOT SYSTEMS; SEVERAL TO MANY STEMS FROM ONE ROOT

Species with multicipital taproots are common at high altitudes. In some cases the stalks are not numerous enough or close enough together to warrant the name "mat plant" or "cushion plant," but in many cases the name is entirely appropriate. The first 5 species below are multicipital root plants which rarely or never occur as mats; the last 3 species form typical mats.

Trifolium dasyphyllum T. and G. grows to a depth of 12 inches (Fig. 11M) among loose rocks in good soil on moist, protected slopes. The taproot had only a few poorly developed laterals. Several short flowering stalks about 1.5 inches high branched from the top of the root.

Phacelia sericea (Graham) Gray developed above ground into a tuft of 3 flowering stalks 5.5 to 8 inches high, with a total spread of 6.5 inches. The much branched taproot (Fig. 11C) descended 9 inches into the rocky soil.

Castilleja brachyantha Rydb., a species rare outside of Colorado and Wyoming, is abundant in certain alpine meadows of Rocky Mountain National Park. It prefers unprotected dry and rocky south slopes. The tough and much branched taproot (Fig. 11P) penetrated an area 12 inches in diameter and to an equal depth. Above ground the average tuft consisted of 8 living and 9 dead stalks from 2 to 6 inches high.

Sedum stenopetalum Pursh (Fig. 4D) and *Arenaria fendleri* Gray (Fig. 4B) have already been discussed in the section on foothill plants, where the development of these species under alpine and foothill conditions have been compared.

Phlox caespitosa Nutt. is abundant on the driest and most exposed boulder fields, where it finds sparing shelter in niches between rocks. Its short stems form dense mats which frequently reach a diameter of 4 or more inches. The root system of a cushion which measured 1.5 by 2.5 inches is portrayed in Fig. 12A. A short taproot descended among the rocks for 9 inches and gave rise to much branched laterals with a total spread of 32 inches.

Similar in habit is *Silene acaulis* L., except that its compact cushions are often large, sometimes reaching 6 inches or even more in diameter. The species is circumpolar and in addition occurs in the alpine belt of the Appalachians as well as in most of the ranges of Europe and Asia. Excavations were made in its typical habitat of rocky soil in the most exposed and windy areas. The coarse primary root (Fig. 12C) had become tough and corky, indicating an age of many years. In every excavation the coarse laterals followed the hill upward at depths of 4 to 6 inches below the surface. It is doubtful if slippage of the soil could account for this unusual root behavior, since the plants were held rather firmly in place by the sandy, rocky soil. Moreover, other mat species in the vicinity failed to show an upward extension of roots.

While the evidence collected is not sufficient to prove that the extraordinary, one-sided root system causes the upward migration of *Silene acaulis,* yet it points definitely in that direction. Wind direction at high altitudes is commonly from lower to higher areas, accounting for the frequent drying up of mats of *Silene acaulis* on the lower side. Although there is no evidence of adventitious roots on any part of the mats, infrequent shoots which grow from points on the lateral roots above the original cushion could easily extend the species upward through the eventual production of new mats at locations above the parent plant.

Eriogonum flavum Nutt. (*E. xanthum* Small) occurs as a dense mat plant in dry, rocky soil in Rocky Mountain National Park at altitudes above 11,000 feet. Typical mats measuring 5 by 7.5 inches were found growing from very tough taproots (Fig. 12B), whose coarse branches extended laterally through 3 feet of soil. Such typical mats averaged 11 flowering stalks standing 1.5 to 2 inches high.

Root Systems; Dwarf Plants with Short Taproots

A considerable group of alpine plants is characterized by a short taproot from which grows a single stem, or in less frequent cases a group of stems.

Heuchera bracteata (Torr.) Ser. occurs sparingly in rocky soil in the mountains of Colorado and Wyoming. Typical plants have 2 or 3 stalks from 6 to 7 inches high growing from a rosette of leaves. A tough, rope-like taproot (Fig. 12F) extends down into the rocky soil to a depth of 16 inches. A few slender branches give the typical root system a total spread of about 4.5 inches.

Senecio taraxacoides (Grey) Greene, a species confined almost entirely to the high peaks of the Rocky Mountains in Colorado, grows best in wet, rocky soil on north slopes. Usually a single leafy flower stalk not more than 3 inches high grows from a branching taproot (Fig. 12M) whose laterals penetrate the soil to a depth of 12 inches, with a total spread equal to the depth.

Rydbergia grandiflora (Pursh) Greene, appropriately known as the alpine sunflower, is one of the commonest species on exposed alpine slopes, in the eastern section of the Rocky Mountain area. Flowering stalks 1.5 to 5 inches high grow from a much branched taproot (Fig. 12G) which penetrates the dry, rocky soil to a depth of 12 to 14 inches.

Sedum rhodanthum Gray, an alpine species common to the Appalachians as well as the Rocky Mountain area, occupies only the most moist habitats and commonly grows with part of its stem covered with water. A plant with 3 flowering stalks from 2.5 to 3 inches high grew from a root system (Fig. 12H) which extended only 5 inches into the wet soil but which spread over an area 14 inches in diameter.

Mertensia alpina (Torr.) Don., a species endemic to high altitudes of the Rocky Mountains, was studied in its usual habitats in very rocky, moist soil, on a protected east slope at an altitude of 11,500 feet. Typical plants consist of a single stalk 4 to 5 inches high, growing from a short taproot (Fig. 12K) with a few very short lateral branches. The entire root system rarely reaches a total depth of one foot.

Erigeron uniflorus L., circumpolar in distribution, grows in moist, rocky soil at altitudes of 10,000 to 13,000 feet in Rocky Mountain National Park. A single flower stalk 2 to 2.5 inches high, extended from a short, fleshy, much branched root which rather thoroughly occupied the soil to a depth of 5 or 6 inches and through a spread equal to the depth (Fig. 11G).

Erysimum nivale (Greene) Rydb., native only to the central section of the Rocky Mountains, was excavated from its typical habitat of moist, rocky soil partially protected by shrubs, at an altitude of 11,000 feet. The coarse, much branched taproot (Fig. 12J), which extended into the rocky soil to a depth of 10 inches, gave rise to 2 or 3 leafy, flowering stalks which rose 6 to 7 inches above the surface of the ground.

Anemone zephyra A. Nels., a species which occurs sparingly in the Arctic, has its center of distribution in the Himalaya Mountains, and is found at high altitudes in nearly all of the principal mountain chains of Asia and Europe, as well as in the Rocky Mountains of North America. In Rocky Mountain National Park it reaches its best development in moist, rocky soil on sunny south slopes. Typical plants have from 3 to 6 stalks measuring 3 to 5 inches in height, growing from a short, thick taproot (Fig. 11Q), with numerous laterals which extend over an area 14 inches in diameter and 6 inches in depth.

Primula angustifolia Torr., rarely found except at high altitudes in the central Rocky Mountains, was studied on a moist, south slope, at an altitude of 11,000 feet. Typically the species consisted of a single flowering stem half an inch tall, growing from a short, thick root (Fig. 11R) with several coarse branches which reached a depth of only 6 inches and a total lateral spread of 9 inches.

Root Systems; Underground Parts Resembling Fibrous Roots

Although plants with true fibrous roots are rarely encountered in the alpine belt, in a few cases the underground parts bear considerable general resemblance to fibrous root systems.

Pulsatilla hirsutissima (Pursh) Brit. occupies dry, rocky habitats at all altitudes from the lower foothills to the alpine belt, although it is much more abundant in the foothills. Probably its occasional occurrence above timberline may be accounted for by the excellent adaptation of its fruits for wind dispersal. Clumps excavated at an altitude of 11,000 feet averaged 5 inches in diameter and had 4 flower stalks 4 to 5.5 inches high. The tough, much branched roots (Fig. 12I) extended downward 16 inches and laterally 3 feet.

Pentstemon glaucus Graham is endemic to the montane belt of the Rocky Mountains but also occurs

infrequently above timberline. The species was excavated from dry, rocky soil on an east slope at an altitude of 11,000 feet. A typical plant of 3 flowering stalks 9 inches high formed a cluster 4.25 by 2.5 inches. Below ground the roots (Fig. 12L) extended downward 14 inches and the lateral spread was more than 3 feet.

DISCUSSION

In many respects ascent from the base to the summit of a mountain in Rocky Mountain National Park is similar to a journey northward at a low altitude. Precipitation and wind velocity increase with altitude, while relative humidity (especially at night), soil temperature, air temperature, and evaporation rate decrease.

Perhaps the most outstanding differences between the effects of altitude and latitude are due to the light relations. Whereas the Arctic has excessively long summer days with light of lessened intensity, the mountains have an alternation of day and night in each 24 hours with light of increased intensity, especially in the violet end of the spectrum. The increase in blue-violet light retards the growth of plants, especially at high altitudes, and is thought to be responsible for the greater development of anthocyanin, which frequently gives a distinct red cast to the foliage of certain alpine plants. Although the length of the growing season is greatly decreased at higher altitudes, the greater intensity of light and the richness in ultraviolet rays are favorable to rapid development of plants and early production of flowers and fruits. Intense light is thought by some to cause the brilliant color of mountain flowers, especially in the alpine belt, but others believe the seemingly intensified color is an illusion due to the drab color of the background. High light intensities probably increase evaporation and transpiration and may thus act as an indirect cause of the low growth habits of alpine plants, although at lower altitudes plants are taller under a higher evaporation rate than obtains in the alpine belt. Another indirect cause of low growth habits is found in the xeric adaptations of alpine plants, especially the thick cuticles and the development of epidermal hairs, both of which absorb such large quantities of light that the percentage of light reaching the chlorophyll layers is materially reduced. On the other hand, such xeric adaptations act favorably by reducing the amount of chlorophyll destroyed by the intense light. Moreover, cloudy weather, especially in the summer, somewhat nullifies the effects of light intensity.

However, the mat habit and the low stature of alpine plants, generally, are not to be attributed to the light factor alone. Wind is unquestionably of great importance in reducing the size of plants, since the espalier habit of trees at timberline is in large part due to the desiccating effects of wind. Destruction of buds and growing tips is a direct result of the drying effect of winds; abrasion of tender parts is frequently accomplished by the blowing of sand. The removal of snow from exposed places by wind in winter is damaging to plants, and the piling up of deep snowbanks which melt slowly through the summer, causes winter killing by a process of smothering. On the other hand, lighter coverings of snow are beneficial and act as a protection against high rates of evaporation as well as sudden temperature changes, and upon thawing, such coverings provide a dependable source of water over considerable periods of time. Moreover, a not too heavy covering of snow reduces the transpiration rate of plants when the soil temperatures are too low to permit adequate absorption.

Although wind is often directly correlated with the rate of evaporation, in Rocky Mountain National Park evaporation decreases directly with increase in altitude, in spite of the fact that wind is greatest in the alpine belt. Thus the daily average evaporation in the growing season of 27.92 cc. in the foothills, 19.22 cc. in the montane belt, and 11.81 cc. in the alpine belt, are conditions entirely in accord with the reduced temperatures of the air at higher elevations. Reduction of evaporation rate with increase in altitude, as determined by standard atmometers, is directly correlated with decreases in the transpiration of plants (Whitfield, 1932, and Sperry, 1936). That lower temperatures both of air and of soil are partly responsible for the low rate of evaporation is a reasonable deduction. Accordingly the suggestion that the rate of transpiration is actually higher in the alpine belt (Coulter, Barnes, and Cowles, 1931, p. 247) seems untenable.

The reduction of evaporation and transpiration rates from foothills to the alpine belt should favor the growth of plants. Likewise increases in precipitation which accompany increases in elevation are factors favorable to growth. It is noteworthy that the greatest reduction in the size of mountain plants is in the alpine belt, where transpiration is least and precipitation greatest.

Daytime relative humidities are slightly highest in the alpine belt, and relative humidities on a 24-hour basis are slightly higher in the alpine belt than in the montane and only slightly lower in the alpine belt than in the foothills. Thus relative humidity is not unfavorable to the growth of alpine plants.

Although absorption from the cold soil is unquestionably reduced to a minimum in the alpine belt, the transpiration rate is also greatly reduced, which balances the low intake of water. From the time of the earlier work of Bonnier, studies of the internal structure and of the adaptations of alpine plants, indicate a rather adequate protection against the severities of the alpine climate, particularly against excessive water losses.

This conclusion is further substantiated by a comparison of the relative extent of roots and shoots in the plants included in the present study. On the basis of greatest length of root and greatest height of stem of the various species studied, the roots of the foothill species constituted 60.41 percent (the stems

39.6 percent) of the total length of the plants, whereas the roots of the alpine species constituted 72.4 percent (stems 27.6 percent) of the total length. These figures are in accord with the findings of Schimper (1903), who concluded that while alpine plants were greatly reduced throughout in size, the transpiring parts of the plants were reduced relatively more than the absorbing parts.

Although the alpine climate is in many respects unique in the temperate zone, and alpine plants are accordingly peculiar in their growth habits both above and below ground, the climate at lower altitudes in the mountains does not differ enough from that of the plains below to produce more than minor variations in the vegetation. The greater rainfall and humidity of the foothills are distinctly favorable to the growth of plants and accordingly herbaceous perennials often make substantial growth.

SUMMARY

The factors of the environment were measured in the upper foothills (altitude 8,000 feet), the upper montane (altitude 10,000 feet), and the alpine (altitude 11,500 feet) belts.

Air temperatures decreased directly with increases in altitude, the alpine temperatures frequently approaching the freezing point during the night even in midsummer, and averaging only 46.21° F. in the daytime. The average daily variation of temperature was about two thirds as great in the alpine belt as in the foothills, with the montane belt intermediate.

Average day relative humidities increased slightly, and average night relative humidities decreased greatly with increases in elevation. However, there were only slight differences between the average relative humidities for the entire growing season in the three habitats: alpine, 63.33 percent, montane, 62.76 percent, and foothills, 66.87 percent.

Rainfall was slightly less in the montane belt than in the foothills, but considerably greater in the alpine belt, where it totalled 7.72 inches for the growing season.

Average wind velocity ranged from 4.5 miles per hour in the alpine belt to 3.16 miles per hour in the montane belt; the foothills were intermediate with an average velocity of 3.66 miles per hour.

The evaporation rate decreased directly with increases in altitude, ranging from an average of 11.81 cc. in the alpine belt, through 19.22 cc. in the montane belt, to 27.92 cc. in the foothills.

The foothill soil consists largely of coarse sand and gravel together with smaller amounts of silt and clay. Soil in the alpine belt is similar except for the large amount of undecayed roots and other plant debris which it contains.

Soil temperatures in the foothills frequently range from 80° F. or more at the surface during the hottest part of the day to from 61 to 68° F. at a depth of 12 inches. At nightfall there is a rapid drop in soil temperature, especially at the surface and in the upper foot of soil. In the alpine belt the soil is almost invariably cold, except at the surface.

The environment is reflected in the growth habits of mountain plants. Growing conditions in the foothills are favorable to the growth both of small and large perennials. Shortness of growing season reduces the number of annuals to a minimum. Species depending upon rhizomes for propagation are common.

Rather deep taproots predominate in the foothills. Through such a root system the plant contacts a permanent water supply. Species are also abundant which have shallow taproots with a wide spread of laterals in the upper soil. This type of root system is well adapted to profit from frequent light showers.

Extreme conditions of the environment in the alpine belt result in a great reduction in the size of the plants; the shoot is reduced even more than the roots. Roots of most alpine plants are extremely shallow, largely in the upper foot of soil and frequently in the upper 3 to 6 inches.

Rhizomes constitute the commonest type of underground systems in the alpine belt; food storage and propagation are well served by the various types of underground stems.

Above ground the alpine species range from an inch or less to about one foot in height. The mat habit is common.

LITERATURE CITED

Bonnier, G. 1920. Nouvelles observations sur les cultures expérimentales à diverses altitudes et cultures par semis. Rev. Gén. Bot. **32:** 305-326.

Clements, F. E., and G. W. Goldsmith. 1924. The phytometer method in ecology. Carnegie Inst. Washington, Publ. **356.**

———, F. L. Long, and E. V. Martin. 1937. Adaptation and origin. Carnegie Inst. Washington, Yearbook **36:** 222-224.

——— 1938. Factor and function in adaptation. Carnegie Inst. Washington, Yearbook **37:** 229-233.

———, and E. V. Martin. 1934. Effect of soil temperature on transpiration in *Helianthus annuus.* Plant Physiol. **9:** 619-630.

Cooper, W. S. 1908. Alpine vegetation in the vicinity of Long's Peak, Colorado. Bot. Gaz. **45:** 319-337.

Coulter, J. M., C. R. Barnes, and H. C. Cowles. 1931. A textbook of botany for colleges and universities. Vol. 3 Ecology. (Rev. by G. D. Fuller.) New York.

———, and Aven Nelson. 1909. New manual of Rocky Mountain Botany. New York.

Cox, C. F. 1933. Alpine plant succession on James Peak, Colorado. Ecol. Monog. **3:** 301-372.

Forsaith, C. C. 1920. Anatomical reduction in some alpine plants. Ecology **1:** 124-135.

Gates, F. C. 1926. Evaporation in vegetation at different heights. Amer. Jour. Bot. **13:** 167-178.

Hanson, H. C., D. L. Love, and M. S. Morris. 1931. Effects of different systems of grazing by cattle upon a western wheatgrass type of range. Colo. Agr. Expt. Sta. Bull. **377.**

Holm, Theo. 1922. Contributions to the morphology, synonymy, and geographical distribution of arctic plants. Rept. Canadian Arctic Exped. 1913-'18, Vol. V, Ottawa.

——— 1927. The vegetation of the alpine region of the Rocky Mountains in Colorado. Mem. Nat. Acad. Sci.: **19.** Third Memoir. U. S. Gov't. Printing Office, Washington.

Livingston, B. E., and F. Shreve. 1921. The distribution of vegetation in the United States as related to climatic conditions. Carnegie Inst. Washington, Publ. **284.**

MacDougal, D. T. 1921. The reactions of plants to new habitats. Ecology **2:** 1-20.

Ramaley, F. 1927. Colorado plant life. University of Colorado.

Raunkiaer, C. 1934. The life forms of plants and statistical plant geography. Oxford.

Robbins, W. W. 1917. Native vegetation and climate of Colorado in their relation to agriculture. Colorado Agr. Expt. Sta.

Salisbury, E. J. 1926. The geographical distribution of plants in relation to climatic factors. Geog. Jour. **67:** 312-335.

——— 1936. The living garden. New York.

Schimper, A. F. W. 1903. Plant geography upon a physiological basis. Oxford.

Shreve, F. 1924. Soil temperature as influenced by altitude and slope exposure. Ecology **5:** 128-136.

Sperry, O. E. 1936. A study of the growth, transpiration, and distribution of the conifers of Rocky Mountain National Park. Bull. Torrey Bot. Club: **63:** 75-103.

Trimble, R. E. 1928. The climate of Colorado. Colorado Agr. Expt. Sta. Bul. 340.

U. S. Weather Bureau, Sec. 23. N. E. Colorado. 1934. Climatic Summary of United States. U. S. Dept. Agr.

Wager, H. G. 1938. Growth and survival of plants in the arctic. Jour. Ecol. **26:** 390-410.

Warming, E. 1909. Ecology of plants. Oxford.

——— 1909. The structure and biology of arctic flowering plants. In Meddeledser om Gronland, Vol. XXXVI. Copenhagen.

Weaver, J. E. 1919. The ecological relations of roots. Carnegie Inst. Washington, Publ. **286.**

——— 1920. Root development in the grassland formation. Carnegie Inst. Washington, Publ. **292.**

———**, and F. E. Clements.** 1938. Plant Ecology. New York.

Whitfield, C. J. 1932. Ecological aspects of transpiration. I. Pike's Peak Region: Climatic Aspects. Bot. Gaz. **93:** 436-452.

——— 1932. Ecological aspects of transpiration. II. Pike's Peak and Santa Barbara Regions: Edaphic and Climatic Aspects. Bot. Gaz. **94:** 183-196.

——— 1933. The ecology of the vegetation of the Pike's Peak Region. Ecol. Monog. **3:** 75-105.